MEASUREMENT AND ANALYSIS OF ARTHROPOD PREDATION ON VELVETBEAN CATERPILLAR, *Anticarsia gemmatalis* Hübner

BY

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DEDICATION

To my wife Elizabeth for her love, commitment, and sacrifice.

"The highest we can obtain to is not Knowledge, but Sympathy with Intelligence. I do not know that this higher knowledge amounts to anything more definite than a novel and grand surprise on a sudden revelation of the insufficiency of all that we called Knowledge before--a discovery that there are more things in heaven and earth than are dreamed of in our philosophy."

Henry David Thoreau 1862

Walking

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Measurement and analysis of arthropod predation on velvetbean caterpillar, Anticarsia gemmatalis Hübner (Lepidoptera: Noctuidae), are presented. Studies conducted during 1981 and 1982 in soybean, Glycine max (L.) Merrill, fields consistently indicated that the 24 hour predation rate of predator complexes on small velvetbean caterpillar larvae remained at approximately 0.4 attacked per predator per day. The impact of various components of predation on the attack rates was examined. While daily per capita predation rate remained essentially constant, the leaf area of the soybean host plant changed dramatically through time. Predator response to changes in the searching universe (i.e., soybean leaf area) was identified to be the key element in predation dynamics.

A model of predation on velvetbean caterpillar larvae in soybean is described. The model integrates velvetbean caterpillar and predator densities, soybean leaf area, and predator searching behavior. The model is validated with three independent field estimates of predation on velvetbean caterpillar larvae. The impact of predation on velvetbean caterpillar population dynamics is investigated by incorporating the predation model into descriptions of velvetbean caterpillar, predator, and leaf area changes. The relative contribution of velvetbean caterpillar, predator and leaf area changes to velvetbean caterpillar population dynamics is detailed.

The study demonstrates that predation on velvetbean caterpillar is intimately related to soybean system changes. The soybean leaf area defines the searching universe of predators. Predation is a function of velvetbean caterpillar and predator number, leaf area, and predator searching behavior. Coupling intensive field research with model analyses allowed for accurate description of predation in this system.

CHAPTER I
INTRODUCTION

Predation is a significant influence on individual prey survivorship, prey population dynamics, community structure, ecosystem energetics, and evolutionary change (Pianka 1974). As an ecological process, predation has been studied and modeled intensively (Holling 1961, Royama 1971, Hassell 1978). The development of predation models has been catalyzed by the incorporation of realistic descriptions of predator and prey behavior (Stimac 1981). In agricultural systems, predation has been identified to be a key component of pest population dynamics (DeBach 1964, Metcalf and Luckmann 1975, Huffaker and Messenger 1976).

Predicting pest population dynamics requires an understanding of the impact of predation. While much attention has been given to the importance of predation in agroecosystems, there are few empirical studies or mathematical descriptions that incorporate the impact of system changes on predation dynamics (Elvin 1983). This critical void in understanding precludes accurate and realistic prediction of pest dynamics and is a contributing factor to the continuing over reliance on pesticides in agricultural systems.

In soybean, Glycine max (L.) Merrill, a defoliating noctuid, the velvetbean caterpillar, Anticarsia gemmatalis

Hübner, has been the object of extensive study (see Ford et al. 1975 for bibliography). Although predation has been identified to be a critical component of velvetbean caterpillar population changes (Shepard et al. 1977, Brown and Goyer 1982, Elvin 1983), to date there exists no mathematical description of predation dynamics in the soybean system. Critical data on the influence of soybean changes on predation on velvetbean caterpillar are lacking, seriously hampering our understanding of predation on velvetbean caterpillar. The present study was designed specifically to investigate the impact of soybean system changes on predation on velvetbean caterpillar and to develop a mathematical model of predation in the soybean system.

The objectives of the present study were to measure the rate of predation by complexes of arthropod predators on a selected velvetbean caterpillar life stage and to develop a mathematical model of predation on velvetbean caterpiller in soybean. Methodologically, this necessitated the coupling of intensive field research, data analysis, and model development. The study is reported in the following six chapters. Chapter II is a review of the pertinent literature on velvetbean caterpillar dynamics in soybean. Models of predation and techniques for measuring predation in agricultural systems are presented in Chapter III. Chapters IV and V present the materials and methods, and results of the study, respectively. Chapter VI describes

the resulting predation model and analyses. Chapter VII summarizes the major findings and conclusions of the study.

Predation in soybean can be understood only in the context of overall soybean system dynamics. By coupling experimental findings with model analyses, the dynamics of predation on velvetbean caterpillar in the soybean system was accurately described. The analytical methodology of the present study is offered as a viable approach to the study of predation in other ecological systems.

CHAPTER II
LITERATURE ON VELVETBEAN CATERPILLAR

Introduction

The velvetbean caterpillar, Anticarsia gemmatalis Hübner, is a highly mobile, polyphagous noctuid (Herzog and Todd 1980, Bushman et al. 1981, Wales 1983). Annually velvetbean caterpillar (VBC) larval populations cause extensive damage to Florida soybean fields (Turnipseed and Kogan 1983). Current control strategies are to apply insecticides when VBC larval populations exceed predetermined thresholds (Strayer 1973, Luna 1979). Because the literature on the velvetbean caterpillar has been reviewed extensively elsewhere (see Neal 1974, Mosoardi 1979, Johnson 1980, Collins 1980, Oliveira 1981, Elvin 1983), this chapter will present a synopsis of VBC dynamics in soybean. Primary emphasis will be on the influence of the soybean system on VBC population dynamics. Included here will be a discussion of the three models (Menke 1973, Luna 1979, Wilkerson et al. 1983) that have been developed to describe specific aspects of VBC dynamics in soybean. The objectives of this chapter are to show the close interrelationships between changes in the soybean system and VBC dynamics and to review only the major components of VBC dynamics in soybean.

Velvetbean Caterpillar in the Soybean System

Temporal Overview

Although VBC dynamics vary in time and space the following is a general rendition of the sequence of VBC dynamics in a "typical," unsprayed (with pesticides) North Florida soybean field.

Velvetbean caterpillar have been hypothesized to overwinter in South Florida, the Caribbean, and Central America, and move northward into the southern United States soybean region each year (Watson 1916, Buchman et al. 1981). Soybean fields are planted in May to June (Anonymous 1976). Adult VBC are found in and around soybean fields by July (Menke and Greene 1976). Larval VBC found in low densities shortly after adult colonization of the area increase rapidly and reach peak densities four to six weeks post colonization. Larval VBC are placed into one of three size categories (Luna 1979). Small larvae, the 1st three instars, are less than 1.27 cm (0.5 in) in length. Medium larvae, the 4th instar, are between 1.27 and 3.81 cm (1.5 in), while large larvae, the 5th and 6th instars, are longer than 3.81 cm. The medium and large larvae are considered to be stages capable of inflicting economic damage (Luna 1979). At high VBC larval densities under proper environmental conditions, an epizootic of the entomopathogenic fungus Nomuraea rileyi (Farlow) Samson can decimate VBC larval populations (Kish and Allen 1978). A second VBC

larval population outbreak may occur in September to October (Luna 1979). Soon after plant senescence (late October), VBC larval populations decline to very low levels (Menke and Green 1976). While VBC are occasionally found post-harvest (November), the onset of colder temperatures (December to January) results in the death of most if not all VBC (Watson 1932, Bushman et al. 1977b). However, if there is an extended period of warm weather, VBC can be found past January. The cultivation of soybean the following spring begins the next cycle of VBC dynamics in North Florida soybean.

Velvetbean Caterpillar/Soybean Interactions

Velvetbean caterpillar dynamics represent a complex interaction of physiological, behavioral, and ecological components. To a large degree, the nature and magnitude of VBC population changes in soybean are determined by the interactions between soybean and velvetbean caterpillar. Accurately describing VBC population dynamics, therefore, depends on adequately detailing the couplings between VBC and soybean. The following is a brief review of the primary interactions between VBC and soybean. Attention is paid to the impact of soybean changes on VBC dynamics.

The soybean agroecosystem is a functional habitat for the VBC, and the soybean plant serves as an ovipositional site and a food source for developing larvae (Watson 1916).

As the plant matures, the nutritional quality of leaves changes affecting VBC development and reproduction (Moscardi 1979). The growth of the soybean plant effects the microclimatic conditions in the soybean field, primarily due to the shading effect of the soybean canopy (Elvin 1983). These changes in microclimate have a significant effect on three major aspects of VBC dynamics: (1) adult colonization rates, (2) onset of fungal epizootics, and (3) survival rates of immature VBC.

Gregory[1] (personal communication) has found a major increase in adult VBC immigration rates after soybean canopy closure. He hypothesizes that amelioration of the microclimate, particularly relative humidity, during canopy closure is conducive to increases in local adult VBC immigration rates. Soybean canopy closure results in microclimatic changes favorable to increased VBC invasion of the soybean field. Increased adult VBC immigration rates contribute to increases in VBC larval populations seen in North Florida soybean fields.

The second effect of canopy closure/microclimate changes relates to N. rileyi epizootics. By canopy closure more adults have entered soybean and oviposit. Subsequently, larval populations soon increase. Canopy closure also increases local relative humidity. One result of changes in VBC density and relative humidity is that conditions for an epizootic of N. rileyi are improved (Kish and Allen 1978). Nomuraea rileyi epizootics can decimate late season VBC larval populations.

The final consequence of canopy closure is a decrease in the mortality rates of VBC immatures that fall to the soil surface. Elvin (1983) has demonstrated that soil surface temperatures, lethal to VBC immatures, are common before canopy closures and result in high mortality rates for VBC that fall to the soil surface. After canopy closes the soil surface temperatures decline, and the mortality rate of VBC that fall to the soil surface declines.

Changes that occur in soybean throughout the season clearly effect VBC dynamics. Although natural enemies are key elements in VBC dynamics (Elvin 1983), the relationship between changes in the soybean system and natural enemy-induced mortality is not well understood. The implications of the lack of critical studies on VBC/soybean interactions are reflected in current management approaches for this insect pest (see Barfield and O'Neil 1984). In the following section, models that have been developed to describe VBC dynamics in soybean will be presented. Particular attention is paid to the descriptions of VBC/soybean interactions in each of the models.

Models of Velvetbean Caterpillar in Soybean

There are three mathematical descriptions of VBC dynamics in soybean (Menke 1973, Luna 1978, Wilkerson et al 1983). Each of these models was developed to achieve different objectives; comparisons of the models must be tempered by consideration of model objectives.

Menke (1973) developed a stochastic simulation model of VBC dynamics in soybean with the objective of detailing the relative impact of immature survivorship, adult immigration rates, and planting dates on percent soybean defoliation. While the model lacks mechanistic descriptions of pertinent ecological processes based on experimental data, model analyses adequately investigate the relationship between VBC colonization success and soybean defoliation levels. Excepting descriptions of larval consumption rates, there are no other VBC/soybean components included in the model.

Luna (1979) developed a short-term predictive model of VBC larval population dynamics as part of a management study of VBC in North Florida soybean fields. The Luna (1979) model couples field estimates of VBC larval densities with larval consumption, survivorship, and developmental rates to predict the number VBC larvae and the damage inflicted to soybean. The objective of this model was to predict VBC numbers and soybean defoliation levels as a tool for management decision-making. The model does not incorporate the mechanisms of VBC dynamics but is an attempt at describing VBC dynamics with respect to economically relevant criteria. The model provides no feedback between VBC and soybean other than VBC consumption of soybean leaf area. Given the limited objectives of the model, the need for extensive VBC/soybean descriptions proved to be unnecessary. The model was calibrated with data derived experimentally and validated with an independent data set.

The most complex model of VBC dynamics in soybean is within the Soybean Integrated Crop Management (SICM) model (see Wilkerson et al 1983) The SICM model was developed to analyze crop management strategies for soybean under conditions of multiple pests and varying weather. The VBC dynamics model is one of several insect sub-models incorporated into the SICM model. Velvetbean caterpillar dynamics are coupled to a mechanistic plant growth sub-model. Leaf consumption by VBC larvae is coupled to defoliation subroutines and integrated with the descriptions of plant production of photosyntate, and ultimately, marketable yield. Soybean defoliation feeds back into the VBC sub-model by driving mortality from food resource limitation. The VBC consumption/soybean defoliation coupling represents the only interaction between the soybean plant growth and VBC population dynamics. Data from studies on VBC reproduction, larval survivorship, and development are used to estimate parameter values for the model. The VBC and soybean submodels have been validated with independent data sets.

The aforementioned models reflect our knowledge of VBC dynamics in soybean. Key processes such as VBC movement, reproduction, and predation have yet to receive the proper study for adequate mathematical description. The lack of critical data limits understanding of VBC dynamics in the soybean system. In this paper the process of arthropod predation on VBC is analyzed from a systems perspective (see Odum 1983). Included in this presentation is a model

of predation on VBC based on field data. Analyses of the predation model unequivocally show the influence of soybean system changes on the process of predation. Results demonstrate that an ecological process like predation can only be understood within the context of system dynamics. In the soybean system, this requires incorporation of plant changes in investigations and descriptions of VBC dynamics. The development of realistic models and ecologically sound management practices depends on an ability to discover how VBC dynamics are affected by relevant changes in the soybean system.

Note

[1]Graduate student, Department of Entomology and Nematology, University of Florida, Gainesville, Florida.

CHAPTER III
LITERATURE ON PREDATION

Introduction

Predation has important consequences beyond the proximal consumption of one organism by another. Predation and the related processes of herbivory and parasitism are strong selective forces for co-evolutionary changes (Pianka 1974). Predation has been identified to be a key element in both population and community dynamics (Clark et al. 1967, Wilson and Bossert 1971, Varley et al. 1973, Pianka 1974). The empirical evidence of classical biological control (DeBach 1964, Huffaker and Messenger 1976), the resurgence of key pests, and the outbreak of secondary pest species (see Metcalf and Luckmann 1977, Bottrell 1979) show the relative importance of predation in agricultural systems.

This chapter reviews models of predator/prey dynamics and the techniques used to measure predation in row-crop agriculture. The primary objectives are to present an overview of the predation literature, to acquaint the reader with the basic components of predator/prey interactions, and to indicate the nature and magnitude of predation in agricultural systems.

Models of Predation

Models of predation can be categorized as those designed to describe predator/prey dynamics in a particular system (e.g., Hughes and Gilbert 1968, Gilbert and Guiterrez 1973, Tamaki and Long 1978) or those designed to describe predator/prey dynamics in general (e.g., Nicholson and Bailey 1935, Lotka 1925, Volterra 1931, Holling 1959, Hassell and Varley 1969). The latter models aid in understanding the components and dynamics of predation that then can be adapted to the specific systems (Holling 1959, 1965).

Models of predation have been reviewed elsewhere (see Royama 1971, Hassell 1978). Following Hassell (1978), this chapter describes the ontogeny of a particular model, the "Nicholson-Bailey" predator/prey model (Nicholson 1933, Nicholson and Bailey 1935). Orlginally formulated as a parasite/host model, the Nicholson-Bailey model has served as a template for considerable model development. Serial improvements in this model have followed closely, sometimes predicting, increased understanding of the behavior and dynamics of predator/prey interactions. A description of the Nicholson-Bailey model will be presented to emphasize properties of model assumptions, structure, behavior, and stability. A description of the major improvements to the model and an indication of the effect of incorporating realistic predator or prey behavior and dynamics will be

provided. Following presentation of the predator/prey models, a discussion of the quantification of predation in agricultural systems is presented.

Nicholson-Bailey Model

The Nicholson-Bailey model, originally developed to describe insect parasitoid/host dynamics, is readily adaptable to describe predator/prey dynamics (Stimac and O'Neil 1983). Arising from Nicholson's "competition curve" (Nicholson 1933), the model describes predator/prey dynamics based on the following assumptions: (1) predators search at random, (2) predator "area of discovery" is a species-specific constant, and (3) predators do not become satiated. The concept of random searching applies to the population of predators, individual predators would re-search areas previously searched by other predators. The "area of discovery" reflects the area effectively covered by a searching predator, which Nicholson (1933) described as constant and a species characteristic. Predator satiation was considered unimportant because the number of prey were conceptualized to be well below levels where satiation would have an affect.

The model was described as a pair of coupled difference equations.

$$N_{t+1} = FN_t e^{-aP_t} \qquad 3-1$$

$$P_{t+1} = cN_t(1 - e^{-aP_t})$$

where P_t is the number of predators at time t, c the conversion rate of prey to predator young, N_t the number of prey at time t, F the prey reproductive rate, and 'a' the predator area of discovery

General model behavior is for increasing fluctuations following local perturbation. Eventually the amplitude of fluctuations drives prey, and shortly thereafter predators, to local extinction. Nicholson (1933) realized that the model did not mimic realistically the long-term stability of many predator/systems in nature. Nicholson (1933) proposed that the model described discrete patches of prey, the stability of the overall predator/prey system a function of asynchronous extinction and growth in the prey patches.

Experimental evidence for the validity of the Nicholson-Bailey model came largely from data gathered in laboratory experiments (e.g., Gause 1934, Burnett 1958a, Huffaker 1958). Varley (1947) claimed field validation of the Nicholson-Bailey model from his study of the parasitoids of the knapweed gallfly, Urophora jacoana (Hering). The conclusions of Varley (1947) were criticized by Milne (1957)

who showed, that, with proper analysis, the results obtained by Varley (1947) did not provide validation of the model. Irrespective of the field validation, predation was obviously more complex than described by the Nicholson-Bailey model (see Hassell 1978). The dynamics of predation was found to be affected by a variety of components not included in the Nicholson-Bailey model. To varying degrees, the model was modified to incorporate these components of predation. The following provides descriptions of the nature and importance of the major components of predation, how the components were included in the Nicholson-Bailey model, and how these modifications affected model behavior and stability.

Modification of the Nicholson-Bailey Model

Prey density. In the Nicholson-Bailey model, predator searching, as encapsulated in the area of discovery (a), was assumed to be a species-specific constant unaffected by changes in prey density. Experimental evidence indicated that this assumption, as well as an unlimited predator appetite, was biologically unrealistic (see Hassell 1978). Data from several studies (DeBach and Smith 1941, Burnett 1954, Ullyett 1949a, 1949b) showed that the number of prey attacked per predator changed as a function of prey density, what Solomon (1949) termed the 'functional response.'

Holling (1959) detailed the nature of the functional response, describing three general attack/prey density

relationships. The Type I responses showed a linear response of predation to increases in prey density (see Figure 3.1: dashed line). The equation describing the Type I response is given by:

$$N_a = a'TN_t \qquad 3.2$$

where N_a is the number of prey attacked, a' the instantaneous search rate, T the time available for search, and N_t the number of prey at time t. Equation (3.2) describes the number of attacks given non-random searching. If predators search at random or prey numbers decrease significantly due to predation, the number of attacks is given by (Hassel 1978):

$$N_a = N_t(1 - e^{-a'T}) \qquad 3.3$$

which is the form of the 'attack equation' of the Nicholson-Bailey model (see Equation 3.1) for one searching predator.

The Type II response (Figure 3.1: dotted line) shows increased attacks with increases in density, though at a decreasing rate. Characterised by the Holling (1959) 'disk equation,' the Type II response describes attacks as a function of search rate (a'), time available for searching (T), prey density (N_t), handling time (T_H). Handling time encompasses the total time to process (capture, kill, eat, etc.)

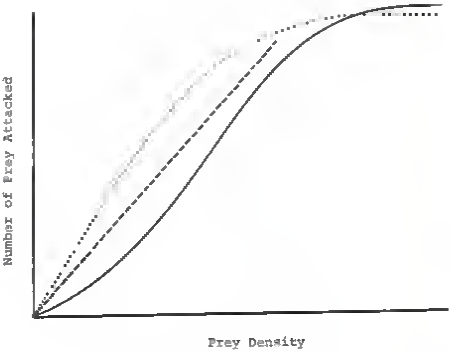

Figure 3 1 Functional responses of predators to changes in prey density Type I response (dashed line), type II response (dotted line), type III response (solid line)

a prey. The equation describing the Type II response is given by:

$$N_a = \frac{a'TN_t}{1 + a'T_H N_t} \qquad 3.3$$

Equation 3.4 describes the number of attacks given replacement or non-random predator searching (Hassel 1978). Equation 3.5 describes the functional response when the above assumptions are not met:

$$N_a = N_t(1 - e^{[-a'(T - T_H N_t)]}). \qquad 3.5$$

For insect parasitoids, the form of Equation 3.5 is slightly different (see Hassell 1978).

The Type III functional response describes a sigmoidal (see Figure 3.1 solid line) relation between predator attacks and prey density. Holling's (1959) original equation:

$$N_a = \frac{bN_t^2 T}{1 + cN_t + bT_H N_t^2} \qquad 3.6$$

where b and c are constants, described non-random searching, and prey replacement. When predators search at random or prey are not replaced, then the number of attacks is given by (Hassell 1978):

$$N_a = N_t\left(1 - e^{\frac{-bN_t(T - T_H N_a)}{1 + cN_t}}\right)$$

In general, arthropod predators have a Type II functional response (Murdoch and Oaten 1975). Incorporating a Type II response into the Nicholson-Bailey model does not provide stability for the predator/prey populations (Hassell 1978). This results from the lack of density-dependent (cf. Smith 1939) predation characterized by the Type II response (Hassell 1978). Inserting a Type III response into the Nicholson-Bailey model will provide for greater model stability, if prey densities remain within the density-dependent region of the Type III response (Hassell 1978)

Holling's (1959) descriptions of the nature and components of the functional response emphasized the importance of incorporating behavior into predation models (see Stimac 1981). The relative importance of particular components of the functional response depends on the characteristics of the system (Holling 1959). Most empirical evidence for functional response descriptions comes from laboratory studies (see Holling 1959, Hassell 1978). As will be shown later, there are significant differences in predator behavior in field versus laboratory systems, especially with respect to the components of predation detailed by Holling (1959).

Predator density. The template for the Nicholson-Bailey model was Nicholson's (1933) "competition curve" which described the relation between the number of predators and number of prey attacked. Nicholson (1933) assumed that randomly searching predators would re-search areas previously searched by other predators. This behavior would lead to an exponential relation between the number of predators and prey attack rates. If predators search non-randomly, a linear relation between predation rate and predator numbers result. Regardless of the nature of the predation rate/predator number relation, the area of discovery (a) remains constant.

Bassell and Varley (1969) described a modification of the Nicholson-Bailey model that incorporated a phenomenon largely found in laboratory studies (Griffiths and Holling 1969, Rassell 1978): mutual interference between searching predators. Examined on a logrithmn scale, as predator number increases searching efficiency decreases such that

$$a = QP_t^{-m} \qquad 3.8$$

where Q is the "quest constant," m the mutual interference constant, and a, P_t as before. Note that when m = 0, Q = a. Inserting equation 3.8 into the Nicholson-Bailey model (3.1) gives

$$N_{t+1} = FN_t e^{-QP_t^{1-m}} \qquad 3.9$$

$$P_{t+1} = N_t(1 - e^{-QP_t^{1-m}}) \qquad 3.10$$

The effect of this modification is to stabilize the Nicholson-Bailey model over given ranges of m, Q, P (see Varley et al 1977, Hassell 1978).

The Hassell-Varley (1969) model has been criticized for being largely a description of predator/prey dynamics in laboratory conditions with unrealistically high predator densities (Griffiths and Holling 1969). Hassell (1978) responded to this criticism by agreeing that while the frequency of inter-predator encounter is higher in the laboratory than the field, the effect of interference was more severe in the field than in the laboratory. In the laboratory, cages isolate predators in one small location. While predators continually encounter one another, they remain in the area where prey are located. In the field, predator density is usually very much lower than in the laboratory. However, when predators encounter one another in the field, one or both may leave the prey area. Hassell (1978) described the various methods predators have of identifying previously attacked prey or searched areas as ancillary evidence of the importance of interference in the field. However, only inferential evidence exists for the importance and occurrence of mutual interference in the field (see Griffiths and Holling 1969, Huffaker et al 1976).

Prey dispersion. An implicit assumption of the Nicholson-Bailey model is that prey are distributed uniformly in space (Hassell 1978). Thus, the probability of a searching predator encountering a prey was assumed to be constant. While this is a mathematical convenience, in nature organisms are rarely distributed uniformly in space (Elliott 1977, Pielou 1977). Closely related to the effect prey distribution has on predator/prey dynamics is the aggregation of predators in areas of high prey densities. The impact of both prey distribution patterns and predator aggregation on the behavior and stability have been described (see Royama 1971, May 1978, Hassell 1978). In general, both contagious prey distributions and predator aggregating responses are powerful stabilizing influences on the Nicholson-Bailey model. As Nicholson (1933) qualitatively described, prey distributions coupled to predator aggregation behavior leads to a continuous "ebb and flow" of predator/prey dynamics. As predators attack one sub-population of prey, causing a decline in prey numbers, other prey sub-populations, free from attack, grow in numbers. The nature and importance of prey refugia was demonstrated mathematically by these models and given strong experimental backing by Huffaker (1958) in an acarine predator/prey system.

Predator switching. The Nicholson-Bailey model describes a one predator, one prey system. In nature,

predators have varying degrees of specificity and may express a preference for one prey species over others. When predators alter choice of prey, they are said to have 'switched" prey (Murdoch 1969, Cock 1978). Switching has important consequences on predator prey dynamics in multi-prey systems (Holling 1959, Murdoch and Oaten 1975, Hasaell 1978). As acceptable prey increase in number, becoming relatively more abundant than other prey, predator switching will result in increased attacks on the growing prey population and decreased attacks on the previously exploited prey. Incorporating switching into a multi-species Nicholson-Bailey framework leads to stability of model behavior (see Hasaell 1978). Experimental evidence for switching comes mostly from laboratory studies (see Cock 1978), but there is evidence for switching under field conditions (e.g., Collins 1980).

Multiple predators. Nicholson and Bailey (1935) used their model to examine multiple predator systems, finding that when more than one predator species was included the model was more stable. Whether multiple predator systems should impart stability to predator/prey dynamics has been the subject of a long, often acrimonious debate (Smith 1929, Turnbull and Chant 1961, Watt 1965, DeBach 1974, Huffaker et al. 1976, Ehler and Hall 1982). Essentially, discussion centers on the importance of interspecific competition among predator populations (DeBach 1974). Mathematical

models, field evidence, and various ecological theories have been marshalled in support of both sides of the multiple species/stability debate (see Varley et al. 1973). While still controversial, the impact of multiple predator species is now largely considered a stabilizing factor on predator/prey dynamics (MacArthur 1955, Rosenzweig and MacArthur 1963, Holling 1973, Odum 1983).

Models that have used the Nicholson-Bailey (1935) model as a template for modeling multiple predator/prey systems include the Hassell (1969) and Comins and Hassell (1976) two predator model, the Hassell and Varley (1969) three predator model, and Gutierrez et al. (1981) generic multiple predator/multiple prey model.

The Nicholson-Bailey (1935) model has been a catalyst for model development, experimental investigations, and theoretical discussions. The Lotka-Volterra (Lotka 1925, Volterra 1931) predator/prey model has undergone similar development (see Hoyama 1971). To define models that are useful in specific systems, proper theoretical structure, provided partially by the development of the Nicholson-Bailey (1935) model, must be coupled to critical experimentation (Baumgaertner et al. 1981). In agricultural systems, modeling past population dynamics requires that ecological processes such as predation be well understood.

The initial step towards an increased understanding of predation is the quantification of the rate of predation over some defined time interval (Stimac and O'Neil 1984).

In the following section, the most commonly used techniques for measuring predation in agricultural systems are discussed.

Quantification of Predation in Agricultural Systems

Diverse methodologies have been used to quantify predation (see Southwood 1978). The techniques used to measure predation in agricultural systems can be categorized as involving:

(1) serology

(2) mark-release-recapture

(3) direct observation

(4) exclusion studies.

Each technique has its set of strengths and weaknesses and provides particular types of information. Below is presented a discussion of each technique, the nature of information obtained, and where feasible, the measured amount of predation.

Serology

Serological techniques utilize the protein specificity and reactivity of antibodies to antigens to identify the presence of prey proteins in predator sera (Boreham 1979). Methodologically, prey antigen (often whole body homogenates) are prepared and injected into laboratory animals which respond by producing antibodies. Antibodies are

extracted and tested for specificity and cross reactivity. Predators are then collected from the field, and their gut contents are tested for reactivity to the antibodies. Positive response indicates the predator has consumed the prey. By knowing the proportion of positive response (P_p), the number of prey consumed per meal (M), and the reaction time duration (T), the number of prey consumed (N_a) can be estimated by (Dempster 1960):

$$N_a = \frac{P_p M}{T}. \qquad 3.11$$

Included in this section are techniques which use radioactivity to identify and quantify predation (e.g., McDaniel and Sterling 1979). Essentially, this technique involves radioactivity labeling and releasing prey, and later testing of field collected predators for radioactivity. Table 3.1 presents a synposis of the results of serological studies that estimated either the proportion of predators attacking prey and/or the number of prey attacked, in agricultural systems. Evident from Table 3.1 is that only a small percentage of predators consume prey during the test period (usually one day), and the quantity of prey consumed per predator is relatively low. The consumption rate per predator is relatively low, with most predators showing no evidence of consuming the target prey over the test interval.

Table 3.1 Summary of quantified arthropod predation in agricultural systems using serological techniques

Prey	Percent positive responses	Predation estimate	Citation
Phytoecta olivacea (Forster)	0.9-9.2	0.0003% available prey per predator per day	Dempster 1960
Erioschira brassicae (Bouché)	0.3-9.1	not estimated	Dempster 1963
Erioschira brassicae (Bouché)	2.5-23.8	6.1 eggs per predator	Coaker and Williams 1963
Multiple prey on broom (Sarothamnus scoparius L.)	0.9-6.5	not estimated	Dempster 1964
Mirids on broom (Sarothamnus scoparius L.)	0.0-25.0 (11 spider spp.)	0.6 per spider per day	Dempster 1966
	0.3-17.4 (7 insect spp.)	not estimated	
Sitona regensteinensis (Köst.)	1.9-33.0	not estimated	Danthanarajana 1969
Buxoa ochrogaster (Guenée)	0.0-31.5	not estimated	Frank 1971

Pieris rapae L.	3.2-33.7	1.6-7.7 attacked by all predators from egg-3rd instar	Ashby 1974
Agrotis ipsilon (Hufnagel)	4.1-10.2	not estimated	Lund and Turpin 1977
Orthotylus adenocarpi (Perris)	3.0	0.16/predator/square meter/day	Boreham and Ohiagu 1978
Heliothis zea (Boddie)	2.8-75	not estimated	Leaiewic et al 1982

Direct Observations

Direct observations are similar to serology in that the identity of the predators is the primary focus of the study. The methodology of direct observations is straightforward. A number of prey are placed in various locations in the field. An observer watches these prey and records any predation events. These observations provide a first hand identification of the predator species attacking a given prey. Closely related to direct observations are observations made on the nature of the characteristic damage done by predators to prey (e.g., Whitcomb and Bell 1964). Characteristic damage can often be sorted into functional groups (e.g., sucking predators), and occasionally to the specific level. Finally, included in the direct observation category are studies which examine predator gut for prey remains.

Phillips and Barber (1933) observed the number of corn earworm, Heliothis zea (Boddie), eggs punctured by a predator, Triphleps (Orius) insidiosus Say, relating the location and density of eggs to the dynamics of the prey species. Davies (1953) dissected the crops of various carabids and identified prey remains (sclerotized body parts) to the family level. Wishart et al. (1956) identified the predators and quantified the level of predation on Hylemya brassicae (Bouché) using direct observations. Turnbull (1960) identified the remains of prey in spider webs, detailing

the components of the spider/prey interaction. Whitcomb et al. (1963), Whitcomb and Bell (1964), Whitcomb (1967), and Lincoln et al. (1967) detailed the natural history of a variety of predators in Arkansas cotton fields. Included in these studies were the identification by direct observations of predators of H. zea and estimates of the quantity of predation occurring in the field. Neal (1974) identified the predators of VBC eggs in Florida soybean fields using direct observation. He also examined gut contents of various predators found in soybean (Neal 1974). Vickermann and Sunderland (1975) combined the precipitin test with gut examinations in a study of predation on arthropod pests of cereals. Buhman et al. (1977a) used direct observation, radiographic tracers and mark-release-recapture to identify the predators and quantify the level of predation on VBC eggs in soybean. Elvin (1983) combined direct observation with mark-release-recapture to describe predation by a complex of predators of VBC eggs and larvae.

In general, direct observations show few predators attacking prey, especially given the relative number of both predators and prey in most agricultural systems. Direct observations may create local disturbance, thereby biasing estimates of the number of attacks. Since direct observation and serology both indicate a low number of attacks (per predator), direct observation appears not to seriously bias the estimated number of predator attacks on prey.

Mark-Release-Recapture

Mark-release-recapture (MRR) techniques are modifications of techniques designed to estimate population densities (e.g., Lincoln index; Southwood 1978). Essentially, MRR entails releasing a cohort of individuals that have been marked in some manner into the field and returning some time later to recapture as many individuals as possible. From the difference in the number of recaptured versus released individuals, an estimate of the mortality during the interval is obtained. Many MRR studies do not have adequate controls for partitioning predation from other mortality sources. Occasionally, MRR is coupled to a life table analysis (e.g., Morris 1959), and predation is recorded as "unaccounted mortality." Several examples will serve to illustrate MRR studies in row crop systems.

Noncontrolled studies. Fletcher and Thomas (1943) measured the mortality of cohorts of Heliothis armergeri (Hübner) eggs and 1st instar larvae. They found that 15 to 33% of all eggs and 12 to 60% of larvae died. Orius insidiosus (Say) was identified, by direct observation, to be a key predator. Dempster et al. (1959) placed pupae of Phytodecta olivacae (Forster) under boards and measured mortality in broom, Sarothamnus scoparius L., fields. Using a combined MRR, sampling, and serological approach, these authors estimated the level of predation. Luna (1979) estimated the mortality of small VSC larvae in soybean as

part of his study of sampling procedures for soybean pest insects. Luns estimated daily mortality to range from 35 to 65%. Elsey (1980) estimated the number of pickleworm, Diaphania nitidalis (Stoll), pupae dying by placing known numbers in cucumber fields for 4 to 8 days. Kennaberry and Clayton (1982) estimated pink bollworm, Pectinophora gossypiella (Saunders), egg mortality by placing a known number of eggs on cotton plants. Egg mortality was associated with egg location and predator number.

Controlled studies. Hughes (1959) measured predation on Erioschirs brassicae (Houché) eggs by identifying the characteristic damage of predatory carabids. He found that 42% of eggs were attacked and estimated that each predator attacked 0.014 of all eggs present. Hughes and Salter (1959) developed a life table of E. brassicae and estimated the amount of predation by subtraction from other mortality sources. Using characteristic damage to identify the predator of the corn earworm, H. zea, Harrison (1960) identified Orius, Coleomegilla, and Chrysopa spp. as key bollworm predators. Harcourt (1966) developed a life table of Pieris rapae (L.), identifying predation via subtraction from other sources. Elsey (1972) studied predation of H. zea eggs using characteristic damage of the predators. He found a positive relation between the number of predatory stilt bugs, Jalysus spinosis (Say), per unit leaf area and the percentage collapsed (attacked) eggs. Stranberg (1981)

used characteristic damage to identify predators of cabbage looper, Trichoplusia ni (Hübner), by the earwig Labidura riparia (Pallas). Stromberg (1981) showed a positive relation between predation and pupal density. Tseng (1982) studied predation of VBC by the predator Eocenthecona furcellata (Wolff) in soybean, relating the presence of the predator to ultimate yields of soybean. Finally, Elvin (1983) used radioactively marked larvae to estimate predation on VBC in soybean. She found that predation rates varied only slightly over three years given major changes in the yearly conditions of the study. Using direct observation, Elvin (1983) also identified the predators attacking specific stages of VBC, finding a remarkable consistency in the species composition of the predators attacking each VBC stage.

In general, MRR studies show arthropod predation can account for a significant level of prey mortality in agricultural systems. Mark-release-recapture studies provide an estimate of the relative contribution of predation to overall prey dynamics. A more direct method is to enclose predators and prey in confined spaces in order to estimate the relative impact of predation. The most common experimental techniques used are exclusion studies that isolate predators and prey in a defined area.

Exclusion Studies

The premise of exclusion studies is to exclude or control all other sources of prey mortality except predation. By carefully isolating predation, its components and dynamics can be closely studied. The technique requires that a barrier prevent escape of predators and prey from a defined area of the host plant. The barrier also serves to exclude unwanted predators or prey from entering the experimental area. In most studies, the barrier of choice has been cages constructed with various mesh screens. Other exclusion materials have been used including insecticides (DeBach 1946, 1955) and ants (DeBach et al. 1950).

Hodek et al. (1965) enclosed sugarbeets with varying densities of the predator Coccinella septempuctata L. and Aphis fabae Scop. as prey. These authors estimated the number of predators necessary to keep prey densities below economic levels. While the experimental design utilized field density of prey inside the cages, the number of predators used (0.5 predators per plant) probably exceeded field levels. Lingren et al. (1968) added Chrysopa spp. larvae and Geocoris punctipes (Say) in various combinations to cages infested with the cotton bollworm H. zea. Prey densities were not determined accurately at the beginning of the study as the cages were seeded not with the immature prey of the two predator species but with adult female moths. Bollworm densities were higher in control cages (without

predators) than in cages with predators. A study by van den Bosch et al. (1969) of predation by three bollworm predators, G. pallens Stal, C. carnea Stephens, and Nabis americaferous Carayon, found a significant reduction in bollworm populations in the presence of the predators. Tamaki and Weeks (1972) used field collected predators, G. bullatis Stal, N. americaferous, and Coccinella transversoguttata Falderman, in a study of predation on three prey species on sugarbeets, under greenhouse conditions that mimicked field conditions. The authors related the effectiveness of the predator to prey density and predator feeding capacity. At high prey densities, voracious predators (e.g., coccinellids) are more effective at attacking prey. At low prey densities, the less voracious predators are more effective. Barry et al. (1974) related predation of G. punctipes, C. carnea, and N. alternatus Parshley on three prey species to soybean defoliation and yield. Although the authors compared the effectiveness of predators at reducing defoliation and yield, the unrealistically high predator and prey densities preclude full applicability of the study. Lopez et al. (1976) studied four predators of two cotton pest insects under laboratory and field conditions. Comparing the effectiveness of the predators for different searching areas, the authors found a dramatic decrease in effectiveness with even small increases in area to search. Frazier and Gilbert (1976) studied predation by Coccinella trifasciata L. on the pea aphid, Acyrthosiphon

pipsum (Harris), in alfalfa. Combining a series of field and laboratory studies, these authors were able to describe aphid dynamics. Predator densities inside of field cages used to study aphid dynamics were much greater than normal field densities. Price and Shepard (1978) studied predation by Li riparia and Calisoma sayi DeJean on noctuid pests in soybean. The predators were shown to have a functional response prey density under minimal searching conditions. McCarty et al. (1980) described predation by a complex of predators on three pest insect species in soybean. Using radiographically labeled prey, the authors were able to aportion total predation among predators. Prey densities, however, did not reflect field densities. Richman et al. (1980) estimated the feeding rates of numerous predators in soybean under high prey [Pseudoplusia includans (Walker)] density regimes. Collins (1980) studied predation by a predator complex attacking VBC and P. includens in soybean. He found that the complex exhibited a Type I functional response (Holling 1959) to changes in prey density. Frazier et al. (1981a) studied the impact of predation on dynamics of A. pisum in alfalfa. Frazier et al. (1981a) were able to describe accurately prey dynamics, although predator densities in the field cage experiments exceeded field levels. Frazier et al. (1981b) used a trapping methodology to cage field densities of predators and A. pisum in alfalfa. The dynamics of the system were described accurately, based on experiments using realistic densities. Reed (1983) examined

predation by a complex of predators on VBC larvae in soybean. Reed (1983) detailed the consumption rate of various predators when both predator and prey densities were very high. Because of the high densities, estimated predator consumption rates probably do not reflect predator consumption rates under field density conditions.

Although exclusion studies can provide data on the components of predation, the majority of studies to date have used unrealistic densities of predators and/or prey and, thus, are limited in applicability. This is especially pertinent in those systems where predators are suspected of being key elements in low density pray dynamics (Elvin 1983). Describing the nature and importance of predation in any given system requires detailed experimentation and analysis (Baungaartner et al. 1981). The experimental design will depend on the type of information desired and the objectives of the analysis. Modeling predation for specific systems requires particular information and an understanding of the interactions among system components. The objective of the present study was to determine the relevant components of arthropod predation on velvetbean caterpillar in the soybean system. The materials and methods of the present study (Chapter IV) were specifically designed to achieve this objective. The results of the present study (Chapter V) were used to describe a model of arthropod predation in soybean (Chapter VI). The analyses of the results and predation model allow an accurate description

of the process of predation in soybeans and have implications to the understanding of predation in other ecological systems (Chapter VII)

CHAPTER IV
MATERIALS AND METHODS

Introduction

The objectives of the present study were to measure the rate of predation on a selected VBC stage by complexes of predators and to develop a mathematical description of predation in this system. The study was conducted over the two year period of 1981-1982. The basic method of study was to measure the rate of predation by complexes of predators on a VBC stage under caged conditions in soybean. The general materials and method of the study will be presented followed by discussions of adjustments made in 1981 and 1982.

General Materials and Methods

All research was conducted on a 0.81 ha field of soybean, variety Bragg, at Green Acres Agronomy farm located 13 km northwest of the University of Florida, Gainesville. The small VBC larval stage was selected as the VBC life stage for study. The small VBC stage was selected because of the number of predators that attack small VBC and because of the relatively high predation rate on small VBC

(Elvin 1983). Because of the size of 1st instar VBC, predation was estimated only for 2nd and 3rd instar VBC. The 24 hour rate of predation by complexes of arthropod predators was estimated by placing complexes of predators and small VBC larvae into cages and measuring the mortality as compared to control cages. Control cages had no predators, only small VBC. The predation rate was estimated by subtracting average control mortality from treatment (with predators) mortality.

Cages used in the study are described by Elvin (1983) and depicted on page 108 of Elvin (1983). Cages were constructed to enclose approximately 91 cm of soybean row and specifically designed to minimize unwanted invasion by aerial, foliage, and ground predators. The foliage was shaken to dislodge arthropods prior to cage enclosure. No insecticides were used at any time during the course of this study. The cages were erected three days prior to conducting an experiment. During these three days, the foliage inside the cages were inspected repeatedly for unwanted arthropods. A minimum of three inspections were made prior to an experiment. The foliage inside the cage was shaken to dislodge inhabitants who were subsequently caught and removed from the cage. Tack-Trap® was applied to the stems of the plants projecting out of the cage bottom. All contact with soybean foliage was minimized both inside and outside of the cages. Holes were patched with tape as necessary

Predator complex composition and densities of small VBC to be used as treatments and controls were determined from sampling data. The cages contained a density of small VBC equal to the mean number of small VBC per 91 cm of soybean row, rounded to the nearest whole number. Predator densities inside the cages were set equal to the sum of the maximum number of individuals per predator species found in any one sample for all predator species found via sampling. Although this led to a higher overall predator density in the cages than the average number found in the field, local concentrations of predators do approach cage densities (see Appendix A). In addition, the small VBC:predator ratios used in the cages were within small VBC:predator field ratios (see Appendix A).

To determine the density of small VBC and predators in soybean, a minimum of 10 samples were taken twice weekly. A 91 cm section of soybean row was shaken over a muslin cloth placed between the rows (see Luna 1979). Only a select group of predators were monitored and chosen for study (see Table 4.1). These predators were chosen because they attack (or were suspected of attacking) small VBC larvae in the soybean canopy, do not nest in the ground, and are present diurnally in relatively high numbers throughout most of the growing season (Neal 1974, Bushman et al. 1977a, Elvin 1983).

Five treatments and one control comprised each of the weekly experiments of the study. Each treatment consisted of a unique predator complex. All treatments and controls

Table 4.1. Predator species used in the present study.

	Species	Family
Spiders	Oxyopes salticus Hentz	Oxyopidae
	Misumenope celer (Hentz)	Thomisidae
	Hentzia palmerum (Hentz)	Salticidae
	Chiracanthium inclusum (Hentz)	Clubionidae
Insects	Geocoris punctipes (Say)	Lygaeidae
	Geocoris uliginosus (Say)	Lygaeidae
	Nabis capsiformis (Germar)	Nabidae
	Reduviolus roseipennis Reuter	Nabidae
	Calleida decora (F.)	Carabidae
	Notoxus spp.[a]	Anthicidae
	Oecanthus spp.[b]	Gryllidae

[a]Only used in 1st weekly experiment in 1981. No demonstrated predation on small VBC larvae

[b]Only used in 1981. No demonstrated predation on small VBC larvae.

were replicated three times. Only field-collected predators and small VBC were used in the study. Predators were collected over a two day period. Those predators collected on the day of an experiment were held individually in capped 7 dram plastic vials. Predators collected the day before an experiment were held overnight in a 66 x 58 x 43 cm wooden cage, provided small VBC (20-40), soybean foliage and moist paper towels. The cage was kept in an outdoor insectary adjacent to the soybean field. Predators kept overnight were recaptured and placed in capped 7 dram vials on the day of the experiment. Due to the high mortality of the predators kept overnight, approximately 50-70% of all predators used in the study were field collected on the day of the experiment. Only adult insects were used, whereas adult and immature spiders were used. Only small VBC larvae collected on the day of the experiment were used in the study.

Adjustments were made to the original treatment designations to incorporate the relative number of predators found over the two day collecting period. The final determination of treatments was a function of sampling data and the success in collecting predators. After determining the treatments, treatments and the control were randomly assigned to the cages. Before placing small VBC or predators in cages, the foliage inside the cages was examined one final time for unwanted arthropods. Both small VBC and predators were examined before placement into the cages, any moribund or dead individuals were replaced with active individuals.

Velvetbean caterpillar larvae were the first placed into the cages, either being gently shaken or placed with a camel's-hair brush onto the foliage. An attempt was made to randomly distribute the small VBC across the top of the foliage. Small VBC were seen to disperse quickly away from the initial point of contact with the plants. Predators were added after small VBC had dispersed. Predators were shaken out of the vials. Care was taken to avoid escape of predators during this time. After placing all predators in the cage, the cage was secured (by zippering the top closed). Total time to place small VBC and predators into a cage ranged from 5 to 10 minutes.

The cages were left undisturbed for 24 hours after which time they were examined carefully for small VBC and predators. Examination of a cage involved cutting plant stems and pulling plants through the bottom of the cage. The plants were then vigorously shaken inside the cage for approximately 30 seconds to dislodge small VBC and predators. The plants were then examined for any remaining inhabitants. The interior of the cage was then examined for small VBC and predators for a 20 minute period. All organisms found in the cage were identified and recorded. Any specimen not readily identifiable was returned to the laboratory for identification. Differences between numbers of small VBC placed in a cage and numbers found after searching were used to estimate the number of small VBC disappearing during the 24 hour period.

Ambient temperature and relative humidity were recorded by a hygrothermograph located approximately 5 m from the field. The hygrothermograph was located in a standard weather box approximately 2 m above ground level. Rainfall was monitored with a rain gauge located approximately 5 m from the field.

Adjustments to Methodology in 1981

Agronomic information for 1981 is shown in Table 4.2. In 1981, two sampling methods were used. A minimum of 10 beat cloth samples were coupled with sweep net samples. The canopy of the row randomly selected for beat cloth sampling was swept 25 times with a 38 cm diameter sweep net (see Luna 1979), and the number of small VBC and selected predators was counted and recorded. After 10 such beat-sweep samples, the number of predator species caught by both methods was compared. If predator species caught in the sweep net samples were different from the species caught in the beat cloth samples, additional beat cloth samples were taken to find the absent species. A total of 20 beat cloth samples were possible. The reason for this approach was the personal observation (using Stimac[1] 1984 unpublished data) that more predator species were caught via sweep net than by beat cloth samples. The sweep net samples were viewed as providing better estimates of the species present while the beat cloth method better estimated the density of

Table 4.2. Agronomic practices 1981, Green Acres Agronomy Farm.

Field size	0.81 Ha
Cover crop:	rye grass
Pre-plant fertilizer:	Muriate of Potash (60%) 113.5 kg/ha
Pre-plant herbicide.	592.5 ml/ha Teflan 887.5 ml/ha Sencor
Planting date.	June 12
Variety.	Bragg
Row spacing:	28 plants/91 cm
Cultivation:	July 13, sweeps July 23, rolling
Irrigation:	June 12, 3.16 ha-cm July 29, 3.16 ha-cm
Yield:	3.775 kg/ha (13% moisture)

predators. By combining the two approaches, a more accurate picture of the nature of the predator complexes in the field could be obtained.

The species composition and densities of predators used in the 1981 study were determined from the bean cloth sampling data. The concepts of species diversity (see Wilson and Bossert 1971, Pianka 1974, Pielou 1977) were adopted to objectively determine the treatments for each weekly experiment. Species diversity encapsulates the numbers and kinds of organisms in a given area. Diversity is maximized when all species are represented by one individual. Diversity is minimized when all individuals belong to one species. Between the maximum and minimum is a spectrum of possible diversities depending on the relative number of individuals and kinds of species present. From the data of the bean cloth samples, the following treatments were designated:

(1) normal diversity--number of predator species equaled the number found in bean cloth samples

(2) maximum diversity--one individual for each predator species found in bean cloth samples

(3) minimum diversity--one species (Geocoris punctipes), number of individuals equaled number in normal diversity treatment

(4) alternative I--unique diversity, number of predator species equaled the number of species found in bean cloth samples

(5) alternative II--unique diversity, number of predator species equaled the number of species found in beat cloth samples.

The number of predators in the "normal" treatment equaled the maximum number of individuals for each species found in any one beat cloth sample. Predator densities in the "alternative" treatments varied to ensure unique diversities

There were two controls used in 1981. Control I had only small VBC; no predators were added to the cages. Control II had no small VBC or predators in the cage. The purpose of Control II was to estimate the number of small VBC in the cages even after all attempts were made to remove indigenous small VBC. Control I estimated the 24 hour mortality rate of small VBC in the absence of predators. Experiments began when small VBC densities reached 5 per 91 cm of soybean row. Seven weekly experiments were conducted between August 10 and October 1.

Adjustment to Methodology in 1982

Agronomic information for 1982 is presented in Table 4.3. Treatments in 1982 were determined from sampling data. No sweep net samples were taken in 1982 because there were few times in 1981 that beat cloth and sweep net samples caught the same number of predators (personal observation) Fifteen beat cloth samples were taken two times weekly.

Table 4 3 Agronomic practices 1982, Green Acres Agronomy Farms.

Field size:	0.81 ha
Cover crop:	lupine and rye grass
Pre-plant herbicide:	1182.5 ml/ha 887.5 ml/ha
Planting date:	June 9
Variety:	Bragg
Row spacing:	76 cm
Plant spacing.	13 plants/91 cm
Cultivation:	July 14, rolling
Irrigation·	June 9, 3 14 ha-cm
Yield:	4.725 kg/ha (10.7% moisture)

Predator treatments were determined as follows:

(1) normal treatment--the number of predators used per species equaled the maximum number found on any one beat cloth sample

(2) other four treatments--the predator number was set equal to the number in the "normal" treatment; species composition different for each treatment.

All five treatments had the same total number of predators per cage but had different species compositions. There was only one control in 1982--small VBC without predators. Analysis of data from 1981 Control II (no small VBC, no predators) indicated few indigenous small VBC present in the cages during the experiments (total of nine small VBC found in 15 cages).

The experiment was conducted weekly from July 8 to September 30. Prior to the time small VBC reached five per 91 cm of soybean row, 10 laboratory reared (see Greene et al. 1976) small VBC were used as the "experimental" density. After small VBC densities in the field exceeded five per 91 cm of soybean row, sampling data determined the experimental cage densities.

The leaf area (cm^2, both sides of the leaves) was measured for 10 plants weekly for 14 weeks (July 6 to October 7). Stems of randomly selected plants were cut at the soil level, and the entire plant was placed in an opaque plastic bag. Plants were then placed on ice for

transport back to the laboratory. The leaf area of all leaves of each plant was measured with a LI-COR® 3100 area meter. The average leaf area per plant was estimated and used to further estimate the total leaf area either in the cages (average leaf area x number plants/cage) or in the 91 cm sampling unit (average leaf area x number plants per 91 cm of soybean row). To determine if there were temperature differences, canopy temperatures inside and outside the cage were monitored with thermocouple probes and an Esterline-Angus® Model PD 2064 Microprocessor.

Note

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CHAPTER V
RESULTS AND DISCUSSION

Introduction

Results are presented in three major sections. Section 1 describes the results of the sampling programs Section 2 shows the leaf area estimates for 1981 and 1982 Section 3 presents the results of the cage studies. Attached as appendices are original data sets and a description of the method of estimation of leaf area in 1981. Appendix A presents the sampling data for 1981 and 1982. Appendix B describes the methodology used to estimate leaf area for 1981 Appendix C presents the composition of the predator complexes, number of small VBC, and 24 predation rates for each treatment replicate in 1981 and 1982. Discussion focuses on data interpretation and implications for an understanding of predation on small VBC in soybean.

Results of Sampling

Shown in Tables 5-1 and 5-2 are the average number of small VBC and predators per 91 cm of soybean row for 1981 and 1982, respectively. Dynamics of small VBC and predators for 1981 and 1982 are shown in Figures 5 1 and 5.2,

Table 5.1. Average number of small VBC, predators, and leaf area per 91 cm of soybean row, and number small VBC per cm^2 leaf area in 1981.

Julian Date	Average number VBC per 91 cm soybean row	Leaf area[a] (cm^2)	Average number VBC per cm^2 leaf area ($x10^6$)	Average number predators per 91 cm soybean row
208	.083	11470	7.236	.666
210	.150	11848	12.660	.350
217	.000	21311	.000	.700
222	.100	30292	3.301	.850
224	1.000	33915	29.485	1.200
229	2.300	40618	56.625	.500
231	4.100	41337	99.185	1.500
236	4.250	41757	101.779	1.100
238	4.700	41224	114.011	2.300
241	4.100	39535	103.548	1.700
245	10.000	38141	259.101	1.334
248	11.615	37693	308.147	2.077
252	15.800	37016	426.842	1.200
255	19.300	36409	530.089	1.700
260	16.300	33847	481.579	2.200
262	21.133	31246	644.338	1.932
266	11.900	24942	477.107	1.500
269	10.600	20207	524.571	2.200
273	7.200	14943	481.831	2.200

[a]Both leaf sides. Estimated with aid of SICM model (Wilkerson et al. 1983: see Appendix B).

Table 5.2. Average number of small VBC, predators, and leaf area per 91 cm of soybean row, and number small VBC per cm^2 leaf area in 1982.

Julian Date	Average number VBC per 91 cm soybean row	Leaf area[a] (cm^2)	Average number VBC per cm^2 leaf area ($x10^6$)	Average number predators per 91 cm soybean row
184	0.000	--	.000	401
188	0.000	--	.000	.133
191	0.000	--	.000	.333
195	0.000	--	.000	.600
198	0.133	16545	8.039	.534
203	0.467	23164	20.161	.468
210	0.267	29660	9.002	1.268
212	0.933	33586	27.779	1.201
216	1.600	40573	39.435	1.001
219	4.133	43810	94.339	1.466
223	8.800	47927	183.613	1.801
226	4.814	50568	95.199	2.202
231	8.667	56111	154.462	3.534
237	11.133	64778	171.864	1.667
240	13.067	60651	215.446	2.067
244	13.867	49508	280.096	1.799
247	17.533	49493	354.252	2.599
251	8.000	55035	145.362	3.135
254	2.400	52550	45.671	2.200
258	2.867	44809	63.983	2.267
261	8.533	40683	209.744	1.400
265	4.262	36300	117.410	1.732
268	2.733	33128	82.498	2.667
272	3.600	28975	124.245	1.667
277	4.467	25998	171.821	1.201

[a]Both leaf sides

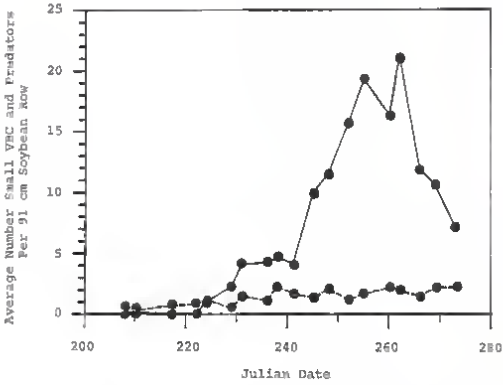

Figure 5-1. Average number of small VBC (solid line) and predators (dashed line) per 91 cm of soybean row from 1981 beat cloth samples

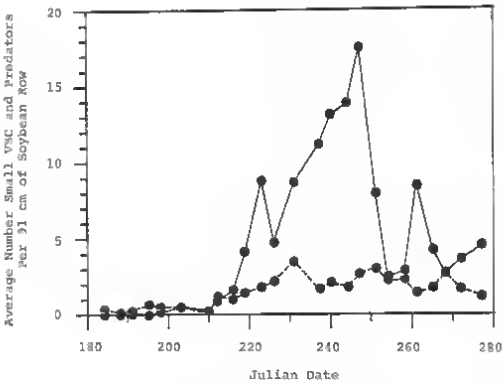

Figure 5.2- Average number of small VSC (solid line) and predators (dashed line) per 91 cm of soybean row from 1982 beat cloth samples

respectively. Small VBC population densities characteristically rise slowly to a peak and thereafter rapidly decline. For 1981 and 1982, the peak small VBC population occurred around Julian day 250 (September 7), reaching densities of approximately 18 small VBC per 91 cm of soybean row. Predator population dynamics show remarkable consistency between and within years. Predator populations slowly rise reaching what appears to be an equilibrium value by Julian day 220 (August 8). Population densities of predators fluctuate around 1.6 (1981) and 2.1 (1982) small VBC predators per 91 cm of soybean row, a density consistently maintained after Julian day 220. Note that there is little consistent relation between small VBC and predator densities. Predator populations were approximately constant during fluctuations of small VBC populations.

There appears to be no numerical response (Solomon 1949) by the predators to changes in small VBC density. Shown in Figure 5.3 is the relation between the average number of predators and the average number of small VBC per 91 cm of soybean row for 1981 and 1982. During both years, population densities of predators were maintained within narrow limits while small VBC populations fluctuate widely.

Leaf Area of the Soybean Canopy

Leaf area (cm^2 of the total leaf surface area) was estimated in two ways during the course of the study. In

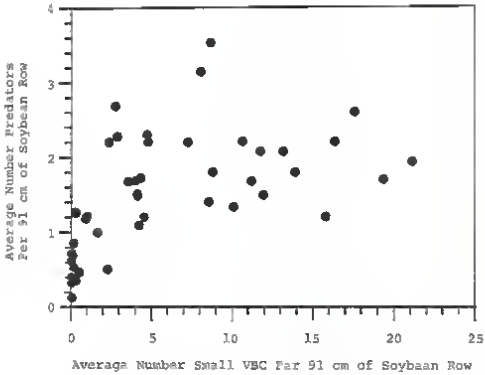

Figure 5.31 Average number of small VBC predators as a function of small VBC density, 1981 and 1982 sampling data.

1981, leaf area was estimated using the Soybean Integrated Crop (SICM) model (Wilkerson et al. 1983). Methodology for this approach is detailed in Appendix B. The leaf area for 1982 was estimated from field samples (see Chapter IV).

Included in Tables 5.1 and 5.2 are the estimated leaf area per 91 cm of soybean row for each sample date in 1981 and 1982, respectively. Leaf area per 91 cm of soybean row can be estimated as the average leaf area per plant times the average number of plants per 91 cm of soybean row. Shown in Table 5.3 and Figure 5.4 is the average leaf area per plant for 1982 as estimated from field samples and the SICM model. As seen from Figure 5.4, there is close agreement between model predictions and the sample estimates of leaf area. Predicted leaf area exceeded the 95% confidence interval of the measured leaf area for only three dates (190, 201, and 238).

Leaf area estimates for 1981 are shown in Table 5.1 and graphically depicted in Figure 5.5. Comparison between Figures 5.4 and 5.5 show similar trends in leaf area growth for 1981 and 1982, though the magnitude of the leaf area was consistently less in 1981 than in 1982. For both years, the leaf area growth was characterized by a linear rise to a plateau and then a gradual descent towards zero at the end of the season. The highest leaf area attained in 1981 was approximately 42,000 cm^2 per 91 cm of soybean row. The maximum leaf area attained in 1982 was approximately 65,000 cm^2 per 91 cm of soybean row.

Table 5.3. Average measured and predicted leaf area per soybean plant in 1982.

Julian Date	Measured leaf area (cm^2 per plant) (SE)[a]	SICM predicted leaf area (cm^2 per plant)
190	580.8 (16.42)	379.7
194	898.6 (59.95)	595.5
201	1703.1 (190.23)	1076.3
208	1979.1 (259.37)	1575.8
215	3037.7 (328.11)	2566.1
222	3619.4 (493.75)	3315.9
229	4093.8 (392.09)	3989.5
238	5093.8 (331.27)	4015.2
245	3593.7 (812.54)	3881.0
252	4339.7 (618.42)	3809.0
259	3298.4 (347.20)	3584.7
266	2708.2 (352.59)	2950.2
273	2149.4 (334.69)	2299.8
280	1887.8 (219.24)	1651.4

[a]Standard error of mean (n = 10).

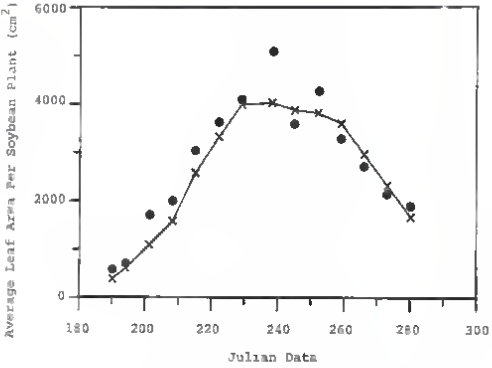

Figura 5 4 Average measured (solid circles) and predicted (x-x) par plant leaf area in 1982.

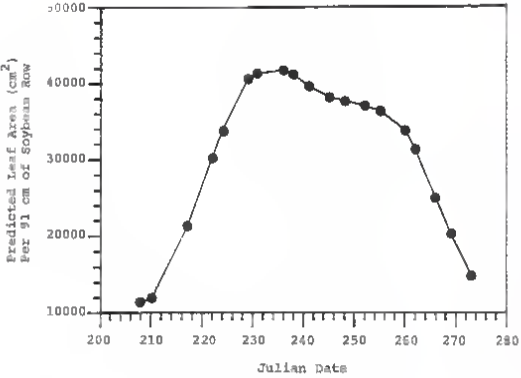

Figure 5.5: Predicted leaf area per 91 cm of soybean row in 1981.

Experimental Results

Treatment results for each weekly experiment are provided in Appendix B. Prior to analysis, predation rates below 1.0 small VBC attacked over a 24 hour period were determined to be too low to differentiate from control mortality. Throughout the remainder of this paper, the predation rates will be with reference to this criterion. Predation rates lower than 1.0 small VBC attacked, therefore, can be considered to be below the resolution of the data set.

In 1981, 47 treatment replications indicated complex predation rates that exceeded 1.0 small VBC attacked per 24 hours. In 1982, 99 treatment replicates indicated predation exceeding the decision criterion. Over the two year period, a total of 72 unique predator complex predation rates were measured. Table 5.4 presents the average predation rates and average control values for each weekly experiment. Control mortality was found by subtracting the number small VBC recovered from the initial number small VBC placed into the cage. This mortality value estimates both the number small VBC dying during the 24 hour interval and the small VBC present but not found when the cage was examined. Since both treatment and control cages were searched in a similar manner by the same personnel, the experimental error associated with finding small VBC are present in both treatments and controls. Since predation is estimated as the difference

Table 5.4. Average weekly predation rate and control mortality estimates for 1981 and 1982.

Julian Date	Predation rate (SE)[a]	Control mortality (SE)
	--- 1981 ---	
232	3.58 (.401)	6.35 (.762)
246	1.83 (.500)	4.67 (1.856)
253	4.08 (.525)	4.00 (1.732)
260	4.86 (.512)	3.00 (1.155)
267	2.67 (.471)	4.33 (1.856)
Average	3.40 (.530)	4.45 (.342)
	--- 1982 ---	
196	2.21 (.389)	1.67 (.333)
204	2.00 (.515)	4.00 (1.155)
210	2.58 (.629)	2.67 (.333)
217	2.24 (.297)	2.33 (.667)
224	2.91 (1.103)	0.33 (.333)
231	2.73 (1.279)	0.00 (.000)
238	4.27 (2.574)	1.33 (.333)
245	4.67 (1.435)	1.33 (.882)
259	3.56 (1.085)	0.00 (.000)
266	3.13 (.765)	1.33 (.333)
273	2.57 (.897)	0.33 (.333)
Average	2.99 (.259)	1.39 (.376)

[a]Standard error of mean.

In control versus treatment mortality, the aforementioned experimental error is eliminated (by subtraction) from predation estimates. The overall average 24 hour control mortality for 1981, 1982 was 4.45 and 1.39 small VBC, respectively. This represents an average of 0.36 and 0.15 proportional mortality of small VBC in control cages for 1981 and 1982, respectively. These values are consistent with other studies of small VBC mortality in the absence of predators (Colline 1980, Elvin 1983). A t-test (Steele and Torrie 1960) showed significant differences between 1981 and 1982 proportional control mortalities at the 5% level ($t = 2.722$, $\alpha = 0.05$).

Average weekly predation rates for the study are presented in Figure 5.6. Note that over a two year period, the average weekly predation rates fell within a narrow range of values. There is no significant difference ($t = 0.705$, $\alpha = 0.05$) between average 1981 predation rates (3.40) and average 1982 predation rates (2.99). These results indicate that the number small VBC attacked during the 24 hour test interval remained relatively constant over a two year period. This is a surprising result given the nature and magnitude of the changes that occurred in the components of predation. During the study, the number of small VBC per cage ranged from five to 16. Predator densities ranged from five to 11 per cage. Average temperature values varied from 19.88 to 28.99°C. The leaf area varied from 15,576 cm^2 to over 65,000 cm^2 per cage. Finally, predation was

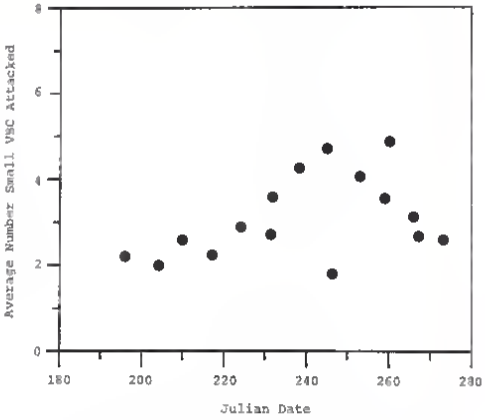

Figure 5.6 Average number of small VBC attacked for each weekly experimental replicate in 1981 and 1982

measured over 72 independent predator complexes. That the 24 hour predation rate changed so little while major changes occurred in the components of predation on small VBC is a significant finding of this research.

Predation on small VBC in soybean appears to be regulated such that the level of predation remains essentially constant through time. Identification of the nature and dynamics of this mechanism will provide a significant contribution toward understanding predation of small VBC. A presentation of the relations among predation and components of predation that could serve as such a regulating mechanism is now relevant. Tables 5.4 and 5.5 describe the data from which the following relations were examined.

Numbers of Small VBC

Presented in Table 5.5 are the initial number small VBC used per cage for each weekly experiment. Figure 5.7 shows the relation between the 24 hour predation rate and the number of small VBC. Evident from Figure 5.7 is that predation rates increased slightly as the number of small VBC per cage increased. Linear regression of predation rates on numbers of small VBC per cage was significant at the 5% level ($F = 8.56$) but with a low R^2 value of 0.38.

However, if the per capita predation rates are plotted against the initial numbers of small VBC (see Figure 5.8), the relation between predator and small VBC number per cage

Table 5.5. Number of small VBC per cage and per cm^2 leaf area, average number of predators, daily temperature and leaf area for each experiment in 1981 and 1982.

Julian Date	Number VBC per cage	Number VBC per cm^2 leaf area	Number predators	Average temperature (°C)[b]	Leaf area per cage (cm^2)
196	10	.00067	8.0	26.11	15776
204	10	.00037	7.0	26.11	27315
210	10	.00026	8.0	27.22	39935
217	10	.00025	8.0	25.56	43941
224	9	.00017	9.0	26.11	54277
231	9	.00014	8.0	25.56	65525
232[a]	11	.00031	7.7	23.88	35400
238	11	.00018	9.0	28.89	62135
245	14	.00028	9.0	27.78	53910
246[a]	10	.00030	8.0	26.38	32883
253[a]	16	.00051	8.7	26.11	31613
259	11	.00026	8.0	25.56	45439
260[a]	16	.00055	9.7	19.98	29448
266	6	.00016	11.0	21.11	39370
267[a]	13	.00064	10.6	21.65	20516
273	5	.00017	5.0	24.44	31996

[a] 1981.

[b] $\frac{\text{minimum} + \text{maximum}}{2}$.

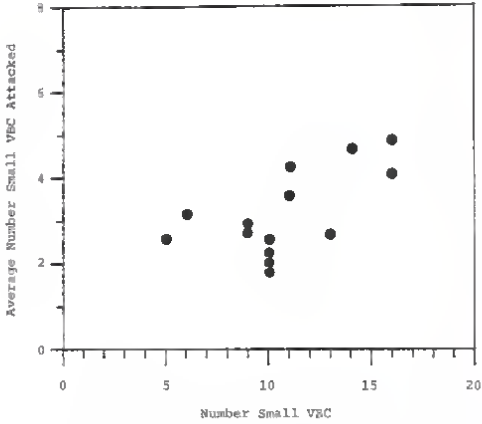

Figure 5.7 Average number of small VBC attacked as a function of the initial number of small VBC for each weekly experiment in 1981 and 1982.

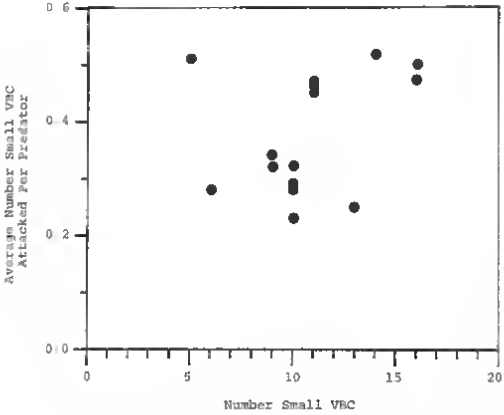

Figure 5.8 Average per capita predation rate as a function of the initial number of small VBC for each weekly experiment in 1981 and 1982.

disappears. The per capita predation rate is based on a per predator basis, a more accurate indicator of the response of predators to changes in key components of predation. Figure 5.9 shows the changes in the per capita predation rate through time. Notice that as with Figure 5.6, the per capita predation rate changes little throughout the season. Figure 5.9 re-emphasizes the point that something seems to regulate predation in soybean. A regression between the per capita predation rate and the initial number of small VBC per cage indicated no significant linear regression model ($P > 0.05$, $R^2 = .107$). There is, therefore, no linear functional response on a per capita basis. Individual predators apparently attack a constant number of small VBC regardless of small VBC density (numbers per cage)

Number of Predators

Figure 5.10 shows the relation between the predator complex predation rate and the number of predators per cage. There appears to be no consistent relationship between predation and the number of predators present ($P > 0.05$, $R^2 = .145$). Figure 5.11 shows the relation between the per capita predation rate and the number of predators per cage. As seen from Figure 5.11, there is no consistent relation between the per capita predation rate and the number of predators present.

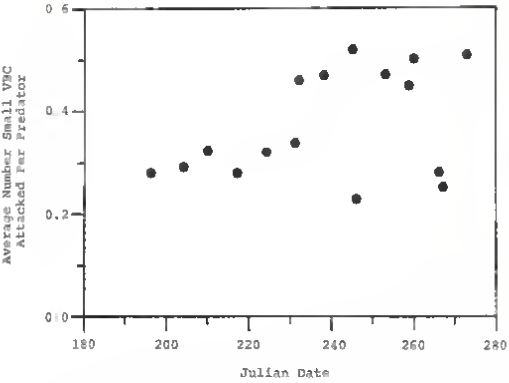

Figure 5.9 Average per capital predation rate for each weekly experimental replicate in 1981 and 1982.

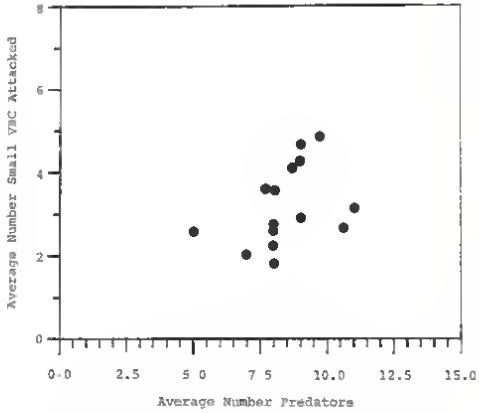

Figure 5-10. Average number of small VBC attacked as a function of the number of predators for each weekly experiment in 1981 and 1982.

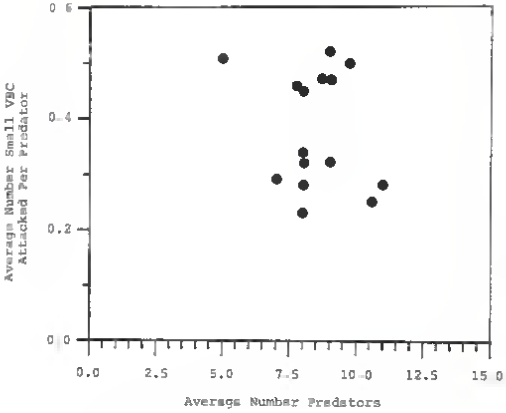

Figure 5.11 Average per capita predation rate as a function of the number of predators for each weekly experiment in 1981 and 1982

Temperature

Relations between predation and temperature are provided in Figures 5.12 and 5.13. Apparently, neither predator complex nor per capita predation rates are effected by changes in temperature. The correlation between canopy temperatures inside and outside the cages showed a significant positive correlation ($r = 0.98$, $P < 0.01$). Comparison of temperatures indicated little difference between canopy temperatures inside or outside of cages.

Leaf Area

Figures 5.14 and 5.15 show the relations between the leaf area per cage and the complex and per capita predation rates, respectively. There appears to be no significant relationship between leaf area and predation ($p > 0.05$). What is evident is that predation does not decrease as the leaf area increases; rather, it remains essentially constant even given major changes in the leaf area. Since the predators must search the foliage to find the small VBC that large increases in leaf area do not result in decreases in predation (on neither a complex nor per capita basis) is a highly relevant finding. As leaf area increases, individual predators must search more area to find small VBC, unless small VBC numbers increase at the same or greater rate than leaf area changes. Shown in Figures 5.16 and 5.17 are the

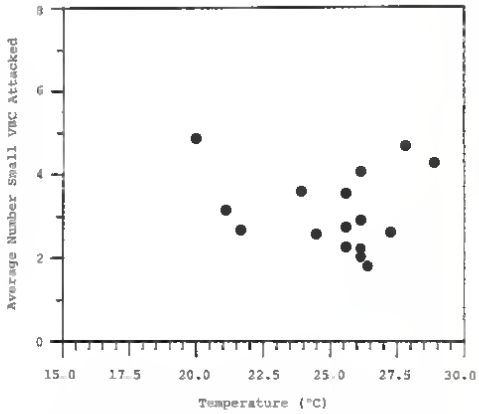

Figure 5 12 Average number of small VBC attacked as a function of the average daily temperature (°C) for each weekly experiment in 1981 and 1982.

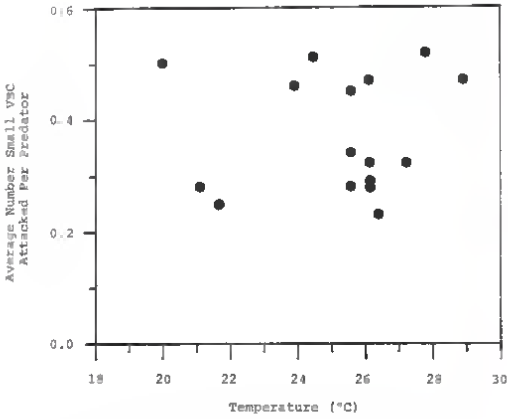

Figure 5.13. Average per capita predation rate as a function of the average daily temperature (°C) for each weekly experiment in 1981 and 1982.

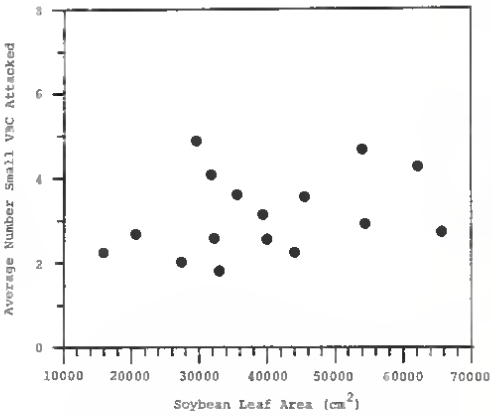

Figure 5.14. Average number of small VBC attacked as a function of the average leaf area per cage for each weekly experiment in 1981 and 1982.

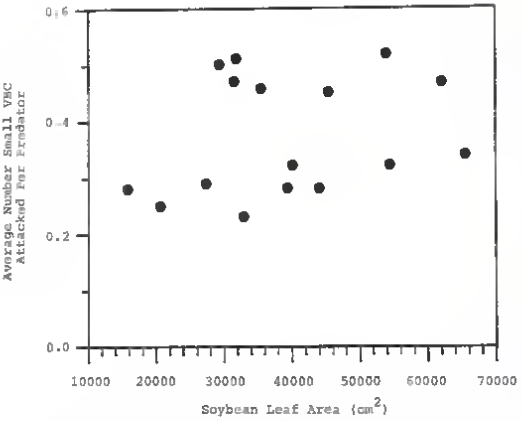

Figure 5.15— Average per capita predation rate as a function of the average leaf area per cage for each weekly experiment in 1981 and 1982.

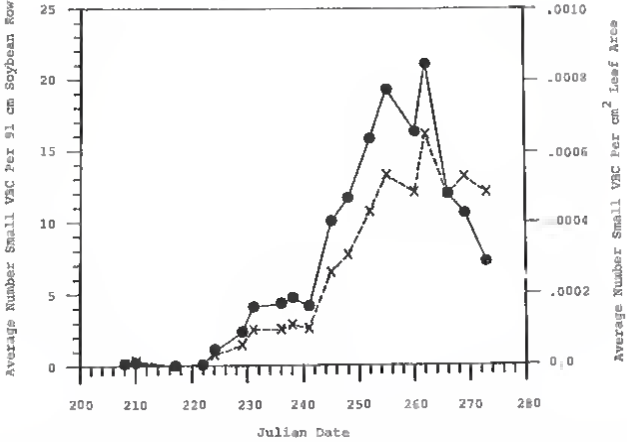

Figure 5.16. Average number of small VBC per 91 cm of soybean row (solid line) and per cm^2 leaf area (dashed line) found per sample in 1981.

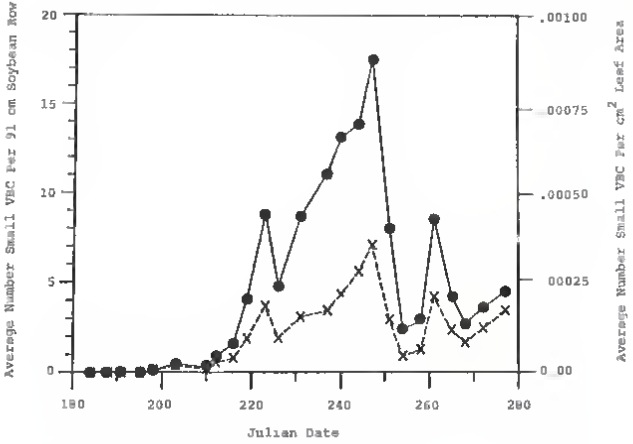

Figure 5.17. Average number of small VBC per 91 cm of soybean row (solid line) and per cm^2 leaf area (dashed line) found per sample in 1982.

densities of small VBC expressed on a per 91 cm of soybean row and on a per cm^2 leaf area (in 91 cm of soybean row) basis for the 1981 and 1982 sampling data, respectively. Note that for both years, the shape of the curve of the number small VBC per cm^2 leaf area largely mimics the shape of the curve of the number of small VBC per 91 cm of row. The similarity in the shape of the curves (within a year) indicates that the effective rate of change in the number of small VBC is similar to the rate of change in the leaf area. However, if the number of small VBC per cage is compared to the number small VBC per cm^2 leaf area per cage, a clear difference exists between the two methods of describing small VBC density. In both Figures 5.18 (1981) and 5.19 (1982), the shapes of the two curves differ markedly, indicating that there is little relation between the number of small VBC on a per cage basis and the number of small VBC on a per cm^2 leaf area basis.

The importance of this distinction between the types of small VBC densities pertains to predator searching abilities. If leaf area increases are not met with corresponding small VBC increases then the number of encounters between small VBC and predators will decrease. Individual predators can only compensate by searching more leaf area. The encounters between predators and small VBC, therefore, depend on the changes in leaf area, small VBC number, and the response of predators to numbers of small VBC per cm^2 leaf area changes. The total area searched by predators can

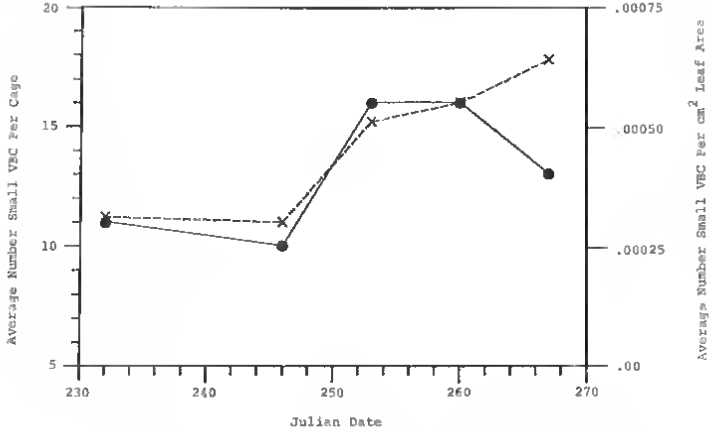

Figure 5.16 Number of small VBC per cage (solid line) and per average leaf area per cage (dashed line) for each weekly experiment in 1981.

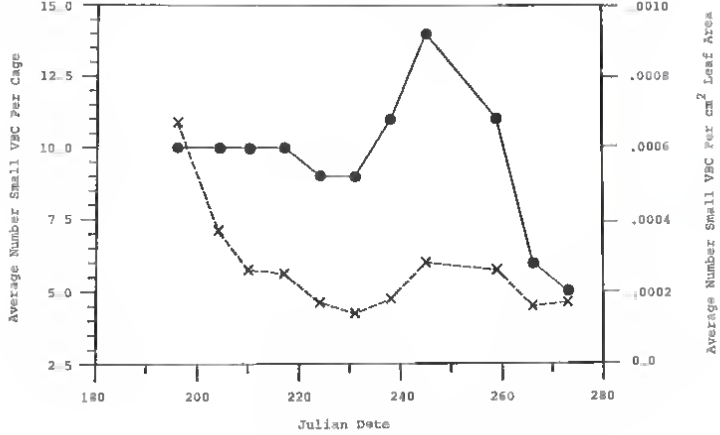

Figure 5.19. Number of small VBC per cage (solid line) and per average leaf area per cage (dashed line) for each weekly experiment in 1982.

be estimated by dividing the number attacked by the number of small VBC per cm^2 of leaf area. Thus, the average area searched per predator is estimated by:

$$S = \frac{N_a A}{VP} \qquad 5.1$$

where,

S = per capita predator search rate (cm^2 per day)

N_a = number small VBC attacked

A = total leaf area (cm^2)

V = number small VBC

P = number of searching predators.

Figure 5.20 shows the relation between the per capita search rate and the leaf area per cage in 1981 and 1982. There is a clear positive linear relation between the area searched by a predator and the leaf area in a cage. As the soybean leaf area increased, the area searched by a predator linearly increased. Plotting the per capita search rate versus the number of small VBC per cm^2 leaf area (Figure 5.21) shows a negative exponential relation of the form:

$$S = C_1 e^{-C_2 V_L} + C_3 \qquad 5.2$$

where;

V_L = number small VBC per cm^2 leaf area

C_1 = maximal search rate above C_3 when $V_L = 0$

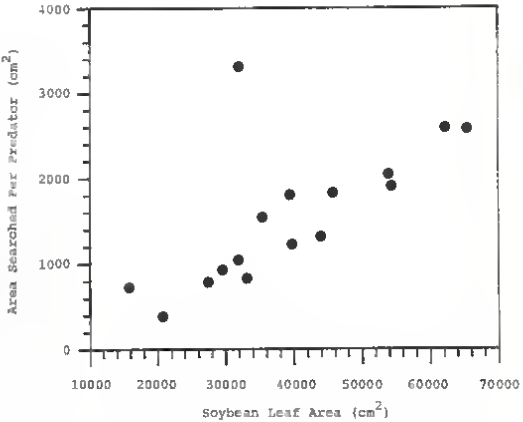

Figure 5.20. Average per capita search rate as a function of the average leaf area in 1981 and 1982.

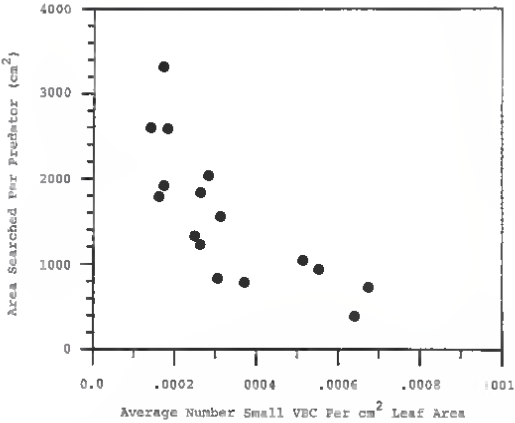

Figure 5.21. Average per capita search rate as a function of the average number small VBC per cm^2 leaf area in 1981 and 1982.

C_2 = rate of decrease in curve (essentially the magnitude of change in predator searching with respect to V_L)

C_3 = minimal area searched at all V_L, the area searched at high V_L

Figure 5.22 shows the relationship between the number small VBC per cm^2 leaf area and the per capita predation rate. Note the consistency of the per capita predation rate as number small VBC per cm^2 leaf area changes. The impact of predator searching behavior in this system is clear. As the number of small VBC per cm^2 leaf area changes, predators alter their search rate. The net result is the consistency of the predation rate shown in Figures 5.6, 5.9, and 5.22.

Figure 5.21 and Equation 5.2 are the templates for a model describing arthropod predation on small VBC in soybean. The changes in predator searching as the number of small VBC per cm^2 leaf area changes, therefore, appears to be the mechanism responsible for regulating arthropod predation on small VBC in soybean. It is critical to recognize that the number of small VBC per cm^2 leaf area can change either through small VBC numerical changes and/or through leaf area changes. Changes in the number of small VBC and the growth of the soybean plant both contribute to setting the prey density important to predation dynamics. The implication of the relation between searching and the number of small VBC per cm^2 leaf area transcends predation on small VBC and

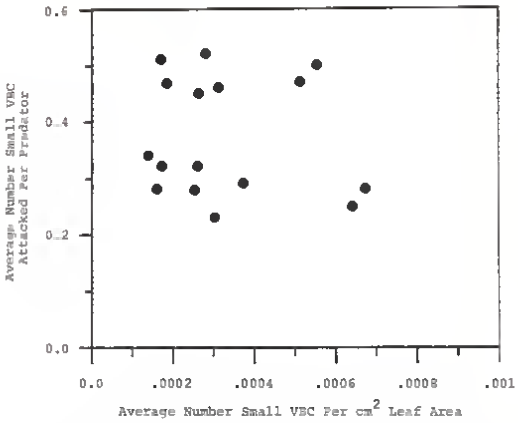

Figura 5.22 Average per capita predation rate as a function of the average number small VBC per cm^2 leaf area in 1981 and 1982.

has ramifications for predation in numerous ecological systems.

CHAPTER VI
MODELING PREDATION IN THE SOYBEAN SYSTEM

Introduction

Adequate representation of ecological processes requires that key components and interactions be identified and described (Holling 1966). For predation, the impact of prey and predator densities, as well as the predator searching and consumption behaviors, has been termed "basic components" (Holling 1959, 1961). Key objectives in describing predator/prey dynamics are to identify the basic components of the predator/prey interaction and to predict the level of predation. In soybean, leaf area and the number of small VBC and predators are the basic components of predation on small VBC larvae (see Chapter V). Ultimately, describing and predicting predation on VBC in the soybean system requires an understanding of predator searching behavior. The changes in the area searched by predators as a function of the number of small VBC per cm^2 leaf area determines the rate of predation on small VBC in soybean (Chapter V).

In this chapter, a model of predation on small VBC is detailed, validated, and subjected to behavioral analyses. The predation model is then integrated with a VBC and

soybean leaf area dynamics model to investigate (1) the relative contribution of predation to VBC dynamics and (2) the influence of VBC and leaf area dynamics on the process of predation in soybean.

A Model of Predation

As the leaf area increased, the area searched by individual predators (S) also increased linearly (see Figure 5.20). When the per capita search rate was plotted as a function of the number small VBC per cm^2 leaf area (V_L), a negative exponential relationship of the form:

$$S = C_1 e^{-C_2 V_L} + C_3 \qquad 6.1$$

was indicated.

Parameter C_1 is the added amount of leaf area searched by a predator above the minimal search rate, C_3, when the number of small VBC per cm^2 leaf area is zero. Parameter C_2 represents the rate of exponential decay to C_3. Data from the 1982 field season (see Table 5.2) was used to estimate the values of the C_i parameters. A non-linear least square regression (Steele and Torrie 1960) of the per capita search rate versus the number small VBC per cm^2 leaf area was used to compute the values of C_1 and C_2. Parameter C_3 was set at 400 cm^2 (per day). The 400 cm^2 represents the lowest average per capita search rate found in either the 1981 or the 1982 data.

The regression model of the per capita search rate as a function of the number of small VBC per cm^2 leaf area was found to be significant ($F < 0.05$) and accounted for 93% of the observed variation (e.g., $R^2 = 0.93$). Non-linear least squares estimated the value of $C_1 = 4556$ and $C_2 = 5045$. Inserting the values of the C_1 parameters into Equation 6.1 gives.

$$S = 4556e^{-5045V_L} + 400 \qquad 6.2$$

Graphical representation of Equation 6.2 and the estimated per capita search rate for 1982 are provided in Figure 6.1. Note that when the number of small VBC per cm^2 leaf area is equal to zero, predators maximize their search rate. As the number of small VBC per cm^2 leaf area increases (either through increases in small VBC or decreases in leaf area), predators progressively search less area, reaching the minimal search rate (C_3) at approximately 0.0007 small VBC per cm^2 leaf area. Knowing the number of small VBC and amount of leaf area, the area searched by the predators can be estimated. Determining the proportion of area searched by a predator allows estimation of the number of small VBC encountered and attacked.

$$N_{ap} = \frac{SV}{A} \qquad 6.3$$

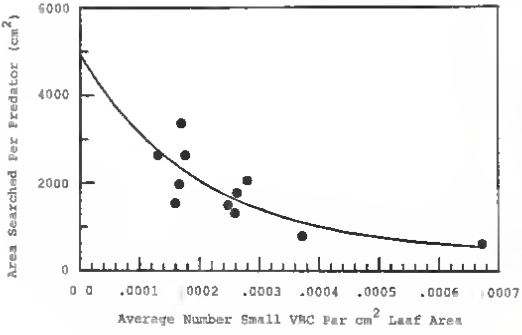

Figura 6.1 - Pradicted per capita search rata as a function of numbar small VBC per cm^2 leaf area. Solid circlas indicate astimatad par capita aaarch ratea for 1982.

where:

N_{ap} = number of small VBC attacked per predator

S = per capita searching rate

A = total leaf area (cm^2 both leaf sides)

V = number of small VBC (per 91 cm of soybean row)

Equation 6.3 estimates the number of small VBC attacked by a single searching predator. Assuming no mutual interference between P searching predators (see Chapter V), the number of small VBC attacked (N_a) is found by inserting Equation 6.1 into Equation 6.3 such that:

$$N_a = PV_L(C_1e^{-(C_2V_L)} + C_3). \qquad 6.4$$

With the C_i values inserted, Equation 6.4 describes the number of small VBC attacked by P searching predators as a function of the number of small VBC, leaf area, and the predator searching behavior. Figure 6.2 shows the graphical form of Equation 6.4 (the "predation model") over a range of realistic field values for the number of small VBC per cm^2 leaf area for one searching predator. Note that over most of the range, a predator maintains an essentially constant attack rate (approximately 0.4 attacks per day). Only at very low numbers of small VBC per cm^2 leaf area (less than 0.00016) does the per capita predation rate go below 0.4 attacks. If P = 1, then Equation 6.4 describes the functional response (Solomon 1949) of the predator to changes in prey (small VBC) densities (number per cm^2 leaf

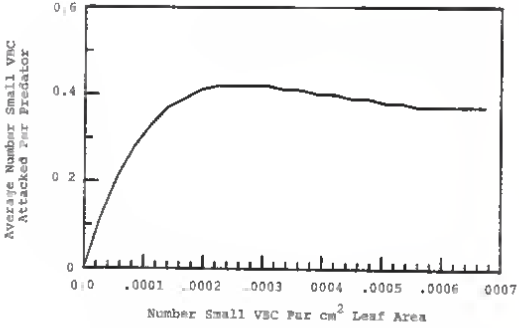

Figure 6.2. Predicted per capita rate as a function of number small VBC per cm^2 leaf area.

area) Examination of Figure 6.2 shows that over the range of small VBC numbers per cm^2 leaf area indicated, the functional response of the predators of small VBC in soybean approximates a Type II response (see Holling 1959).

Model Validation

Data from 1981. The 1982 data were used to estimate the values of the C_1 parameters and, thus, describe the predation model (Equation 6.4). The 1981 data, not being used to develop the predation model, can be used as an independent validation for the model (Overton 1977). The validation procedure followed here will be to use the predation model to predict the 24 predation rate by arthropod predator complexes on small VBC larvae in soybean measured in 1981. Inputs for the predation model will be the number of small VBC and predators and the leaf area for each replicate in the 1981 experiments (see Table 5.1). Statistical comparison (t-test: Steele and Torrie 1960) of model prediction versus average weekly predation rates on small VBC in soybean will serve as the basis for acceptance of model validation.

Measured and predicted predation rates for each 1981 replicate are given in Table 6.1. Measured and predicted average weekly predation rates for 1981 and 1982 (Table 6.2) are provided. Statistical comparison (t-test: Steele and Torrie 1960) for 1981 show no statistical significance

Table 6.1. Measured and predicted predation rates for each replicate of the study in 1981.

Julian date	Measured predation	Predicted predation
232	2.75	3.34
	2.75	3.34
	2.75	3.75
	4.75	2.92
	3.75	2.92
	4.75	2.92
246	1.33	2.09
	3.33	2.92
	1.33	4.20
	1.33	4.20
253	5.00	4.18
	4.00	4.18
	3.00	4.18
	1.00	4.56
	5.00	4.56
	3.00	4.56
	2.00	1.90
	4.00	1.90
	7.00	3.04
	4.00	3.04
	4.00	2.28
	3.00	2.30
	8.00	2.28
260	5.00	4.08
	2.00	4.12
	6.00	4.12
	5.00	4.87
	6.00	4.87
	7.00	4.87
	3.00	1.87
	4.00	1.87
	2.00	2.70
	4.00	2.62
	3.00	2.62
	6.00	4.21
	7.00	4.12
	8.00	4.12

Table 6.1--continued

267	1.67	2.65
	2.67	3.34
	1.67	4.45
	2.67	4.45
	2.67	4.08
	6.67	4.08
	1.67	4.08
	2.67	4.08
	2.67	4.08
	1.67	4.08

Table 6.2 Comparison between average measured and predicted predation rates for 1981 and 1982

Julian Date	Average predicted predation rate (variance)	Average predicted predation rate (variance)
	--- 1981 ---	
232	3.58 (.97)	3.20 (.12)
246	1.83 (1.00)	3.35 (1.07)
254	4.08 (3.60)	3.30 (1.19)
260	4.86 (3.70)	3.65 (1.17)
267[a]	2.67 (2.20)	3.94 (.30)
	--- 1982 ---	
196	2.22 (1.36)	1.92 (.01)
204	2.00 (1.60)	2.84 (.01)
210	2.58 (1.58)	3.32 (.01)
217[a]	2.24 (.60)	3.35 (.01)
224	2.91 (2.70)	3.51 (.02)
231	2.73 (4.00)	2.92 (.04)
238	4.27 (4.30)	3.58 (.01)
245	4.67 (7.00)	3.71 (.01)
253	3.56 (2.00)	3.28 (.01)
266[a]	3.13 (1.60)	4.18 (.09)
273	2.56 (1.40)	1.91 (.03)

[a]Significant difference ($P < .05$) between measured and predicted predation rates as judged by a t-test (Steele and Torrie 1960)

between model predicted and measured average weekly predation rates for four of five comparisons. The only significant difference between model prediction and measured average weekly predation rates occurred on Julian day 267 in 1981. The t-statistic for this date was 2.542 compared to the tabular t-value of 2.262 (Steele and Torrie 1960, $n = 10$, $\alpha = 0.05$). The close similarity between t-values justify accepting the null hypothesis that there is no significant difference between model prediction and measured predation rates, avoiding a Type II error. The model can, therefore, be judged an adequate description of the process of predation on small VMC in soybean as judged by comparison to an independent data set. Additional confirmation of the descriptive ability of the model can be seen in Figure 6.3. Plotting the measured and predicted average weekly predation rate for 1981 and 1982 versus time shows the close similarity in the predation rates and in the temporal dynamics for measured and predicted predation rates. Of 15 possible changes in the week-to-week dynamics (both years), 13 show common directional changes, indicating that the model accurately mimics the temporal dynamics of the data.

Further evidence for the validity of the model can be seen in Figure 5.21 where the plot of the per capita search rate as a function of the number small VMC per cm^2 leaf area for 1981 and 1982 is provided. Note from Figure 5.21 that all points for 1981 and 1982 follow a consistent pattern--a negative exponential decay. For both years, the same

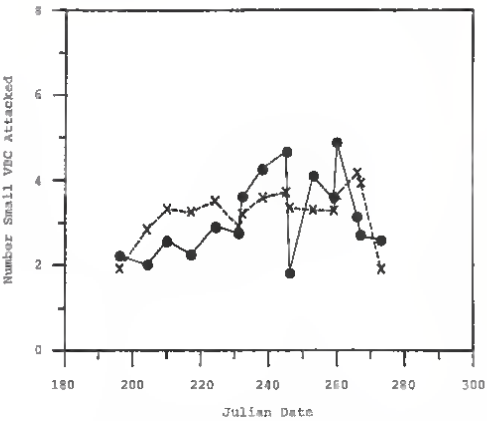

Figure 6.3. Predicted (dashed line) and measured (solid line) average weekly predation rates for 1981 and 1982.

relationship is demonstrated between predator search rates and the number of small VBC per cm^2 leaf area. Non-linear least squares (Steele and Torrie 1960) estimates of the C_i parameters for the combined 1981/1982 data are C_1 = 4515, C_2 = 5045 with C_3 again set at 400. There is a slight improvement in the R^2 value for the combined 1981/1982 data (0.94 versus 0.93 for 1981); thus, the above C_i values will be used throughout all remaining model analyses and discussions.

Elvin (1983) data. Additional data for validating predictions from the predator model (Equation 5.4) can be found in Elvin (1983). She estimated the 24 hour predation rate of small VBC in soybean using a modified mark-release-recapture technique (see Chapter III). Data for two years (1981 and 1982) of Elvin (1983) are detailed enough for the present validation procedure. That work was conducted in a 0.81 ha soybean field located less than 10 m from the soybean field of the present study. Estimates in the present study for leaf area, predator and small VBC densities in 1981 and 1982 can be used to estimate the 24 hour rate of predation on small VBC larvae released into soybean foliage by Elvin (1983). The validation criteria are that: (1) model predictions mimic the temporal dynamics seen in the Elvin (1983) data and (2) the model be able to predict the 24 hour rate of predation on small VBC in soybean measured by Elvin (1983) to within one attack by all predators over 24 hours.

Predicted and measured predation rates for 1981 and 1982 are shown in Tables 6.3 and 6.4, respectively. Initial predation rates more closely approximate the measured predation rates in the latter part of the soybean growing season. Note that both the model and the measured predation rates indicate an attack rate less than 1.0 small VBC by all predators in 24 hours for 13 of 19 comparisons. Recall that for the present study, 24 hour predation rates less than 1.0 were said to indicate that predation had not occurred. Applying the same criterion to the present analysis (13 of 19 comparisons), both the Elvin (1983) data and the model predicted predation rates give similar results--that little or no predation occurred in the soybean foliage over a 24 hour period.

As is evident from Tables 6.3 and 6.4, initially the model does not adequately estimate early season rates of predation of small VBC. Elvin (1983) estimated much higher levels of predation than predicted by the model. However, if the number of small VBC released is taken into account, the discrepancy between model predictions and actual predation rates decreases considerably. Elvin (1983) released between six and 10 small VBC regardless of the small VBC field densities present at the time. Only later in the season (see Tables 6.3 and 6.4) did Elvin (1983) release densities approximate to field densities. Earlier in the season, release densities greatly exceed the field densities. Essentially, there were two phases of the Elvin

Table 6.3. Comparison between Elvin (1983) and predicted predation rates in 1981

Julian date	Measured predation	Number small VBC released	Sample number VBC	Sample number predators	Leaf area (cm^2)	Predicted predation	
						Initial	Adjusted
209	2.00	10	.12	.51	11768	.20	2.03
216	1.83	10	.02	.70	19624	.27	1.74
223	1.17	10	.55	.70	32000	.29	.99
230	.00	10	3.20	1.00	41120	.42	.84
237	.50	10	4.48	1.70	41591	.71	1.24
244	.00	10	8.53	1.43	38318	.60	.70
251	.00	10	14.75	1.42	37229	.60	.39
258	.00	7	17.50	2.00	36028	.81	.31

Table 6.4. Comparison between Elvin (1983) and predicted predation rates in 1982

Julian date	Measured predation	Number small VSC released	Sample Number VSC	Sample number predators	Leaf area (cm^2)	Predicted predation	
						Initial	Adjusted
187	2.59	7	.00	.20	4883	.12	1.41
194	3.00	10	.00	.53	7741	.28	3.37
201	.40	7	.33	.49	20516	.20	.76
208	.37	6	.32	1.04	27804	.43	1.05
215	.00	10	1.43	1.05	38826	.44	1.12
222	.00	7	7.63	1.72	46898	.65	.61
229	.41	9	7.13	3.00	53894	1.17	1.36
236	1.40	9	10.72	1.98	63334	.73	.65
243	.00	10	13.67	1.87	52294	.76	.57
250	.00	10	10.38	3.00	53650	1.21	1.1[illegible]
257	.60	6	2.63	2.25	46744	.80	1.[illegible]

(1983) study. (1) high density release in low density areas and (2) releases at approximate field densities. Therefore, adjustments to the validation procedure were necessary to incorporate the experimental protocol of the Elvin (1983) study.

When VBC are placed into a soybean field at or near field densities, the resulting rate of predation should approximate actual field levels. If, however, the density of VBC placed into a field is higher than endemic field densities, higher predation rates would be expected. This is because predators keying their search rates to endemic numbers of small VBC per cm^2 leaf area would have a higher probability of finding the locally high density. Lower numbers of VBC per cm^2 leaf area would lead to higher proportions of the leaf area searched, eventually leading to more of the "high density" (released) VBC being found by the predators. Both Elvin[1] (personal communication) and Collins (1980) have noted predator aggregation at release sites when the number of VBC released are higher than endemic field densities.

Incorporating the dichotomy between Elvin's (1983) release densities and the endemic field densities requires estimating the per capita search rate as a function of the number of small VBC per cm^2 leaf area indigenous to the field, than using that search rate to estimate the number of released VBC attacked. Mathematically, the process of estimating the number of attacks can be expressed by

$$N_{aR} = \frac{S_i N_R F}{A} \qquad 6.5$$

where;

N_{aR} = number of released small VBC attacked

S_i = area searched by a predator as a function of the indigenous number of small VBC per cm^2 leaf area

N_R = number of released small VBC

F = number of searching predators

A = soybean leaf area.

Tables 6.3 and 6.4 show the measured (Elvin 1983) and predicted predation rates, incorporating the effects of release versus field density differences for 1981 and 1982, respectively (see "adjusted" column). Plotted in Figure 6.4 are the measured and (adjusted) predicted predation rates for 1981 and 1982. There is close agreement between the predicted and the measured predation rates. The magnitude and temporal dynamics of predicted predation rates closely approximates measured predation values. Both predicted and the measured predation rates decline with time. The highest predation rates are seen earlier in the season when the difference between released and endemic small VBC densities are most pronounced.

The model has, therefore, satisfied the first validation criterion by mimicing the temporal dynamics of predation as measured by Elvin (1983). The second validation criterion was that the model be able to predict the 24 hour

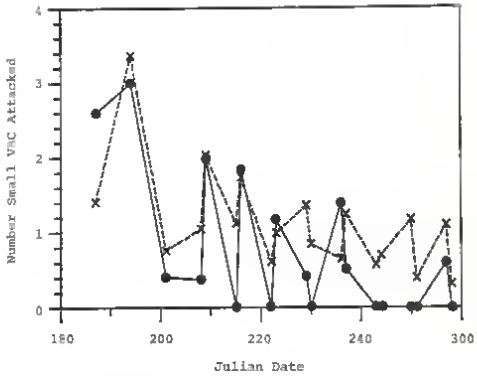

Figure 6.4 Predicted (dashed line) and measured (solid line) average weekly predation rates for 1981 and 1982, Elvin (1983) data.

predation rate to within 1.0 small VBC attacked by all predators. Comparison between the adjusted predicted predation rates and the Elvin (1983) data show that for 16 of 18 comparisons, the model predicted to within 1.0 attack the 24 hour predation rate. The average difference between model prediction and Elvin (1983) data was 0.41 and 0.76 attacks in 1981 and 1982, respectively.[2]

Thus, both validation criteria have been satisfied, and the model can be said to be an adequate representation of Elvin (1983) data. Overall, the predation model has been validated with three independent data sets and, therefore, can be judged an adequate description of the process of arthropod predation on small VBC in soybean. Significantly, predation on small VBC in soybean was shown to be primarily a function of predator searching not predator consumption behavior. The ability of predators to find prey not the ability of predators to process prey is the decisive factor in determining the level of arthropod predation on small VBC in the soybean system. The importance of this finding to the study of predation in other systems will be discussed in Chapter VII. Results of behavioral and sensitivity analyses (see Overton 1977) conducted on the predation model are presented below.

Predator Modal Behavior

Equation 6.4 describes the mathematical form of predation on small VBC in soybean. Components of predation in the soybean system are (1) the number of searching predators, (2) the number of small VBC present, and (3) the total leaf area to search. To investigate the contribution of each component to predation on small VBC, realistic, progressive changes will be made independently to each component and the effect on predation measured. A "nominal" value of predation based on one predator searching for 10 small VBC in 35,000 cm^2 of leaf area will be calculated and used for comparison purposes. The nominal values for small VBC, predators, and leaf area represent reasonable values that are found commonly in soybean fields occupied by small VBC. Following these analyses, the impact of changes of the parameters, C_1, on model behavior will be described. In the final section of this chapter, Equation 6.4 will be coupled to a description of VBC dynamics in soybean, and the role of predation in this system will be investigated.

Nominal values. Given one searching predator, 10 small VBC, and 35,000 cm^2 of leaf area, the model estimates a per capita predation rate of 0.42 attacks in a 24 hour period. In each of the following three figures (6.5, 6.6, and 6.7), the nominal value will be indicated by a solid circle.

Predator number. The influence of changes in predator number were examined by estimating the rate of predation for one to 10 predators (VBC and leaf area constant), a realistic range of possible predator densities in 91 cm of soybean row. As seen in Figure 6.5, there is a linear relation between predator number and the predation rate. The model indicates no influence of mutual interference between searching predators (see Hassell and Varley 1969). In Chapter V, the analysis of the relation between the predation rate and the number of predators showed no evidence for mutual interference over the density of predators used in the study. The two year sampling program showed that at no time were more than 10 small VBC predators found in any 91 cm of soybean row (see Appendix A). Average predator densities during this time were consistently less than this maximum density. Given that there was no evidence for interference in the cage studies, which used higher than field predator densities, the linear predator/predation rate relation in this system seems an accurate description.

The model predicts that for a given VBC and leaf area regime, increases in predator number will result in higher predation rates. The magnitude of predation will be a linear function of predator number. For the nominal case, one predator is expected to attack 0 42 small VBC per 24 hour period (one per 2 4 days). At higher predator densities (e g , in field cages), 10 predators would attack 4 2

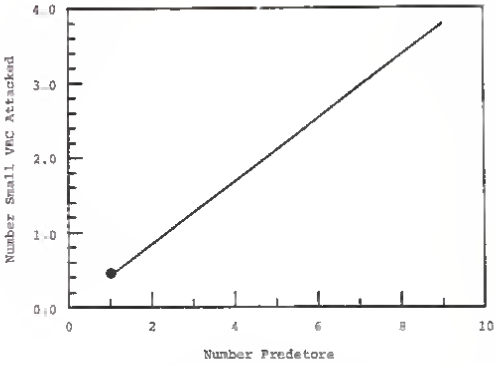

Figure 6.5— Per capita predation rate as a function of the number of predators. Nominal value indicated by solid circle. Leaf area and small VHC number held constant.

small VBC. Note the impact of leaf area here. Even given 10 searching predators, less than 50% of the small VBC present are attacked. Ten small VBC per 91 cm of soybean row would be considered a substantial (but still non-economic) density (Luna 1979). At realistic field predator densities, two to three per 91 cm of soybean row (see Figures 5.1 and 5.2), predators would search only enough leaf area to attack 12.6% of the small VBC present (3 predators x 0.42 attacks per predator = 1.26 attacks. (1.26 attacks/10 small VBC) x 100 = 12.6%].

Number of small VBC. The relation between the 24 hour predation rate and the number of small VBC (range: 0 to 50) per 35,000 cm^2 leaf area is shown in Figure 6.6. There appear to be three distinct regions of model behavior. From 0 to 10 small VBC, the predation rate increases as the number of small VBC increase, though at a decreasing rate. From 10 to 24 small VBC, the predation rate decreases slightly from 0.42 to 0.37. From approximately 25 to 50 small VBC, the predation rate increases, linearly after approximately 34 small VBC.

Region I of model behavior (0 to 10 small VBC) reflects the increase in predation as the number small VBC per cm^2 leaf area increases from 0.0 to 0.00029. Although predators search progressively less area as the number of small VBC per cm^2 leaf area increases (Figure 6.1), the relative change in the numbers of small VBC number versus the

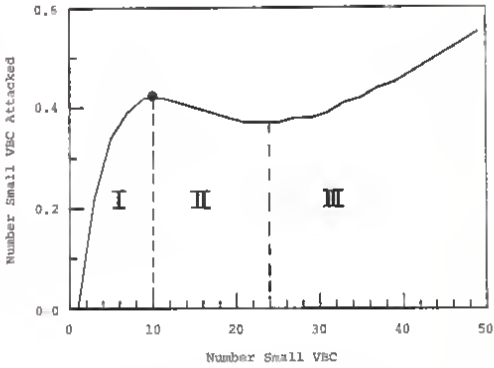

Figure 6.6: Per capita predation rate as a function of the number of small VBC. Nominal value indicated by solid circle. Leaf area and predator number held constant.

proportional increase in the area searched by the predator results in more small VBC attacked. Between 0.00003 (1/35,000) and 0.00029 (10/35,000) small VBC per cm^2 leaf area a predator searches between 4309 cm^2 (at one VBC) and 1468 cm^2 (at 10 VBC) of leaf area. At one small VBC per 35,000 cm^2 leaf area, the predator searches approximately 12.3% of the total area (4309/35,000). At 10 small VBC per 35,000 cm^2 leaf area, a predator will search approximately 4.2% of the leaf area (1468/35,000). As the number of small VBC increases, there is an approximate 3-fold decrease in the area searched by predators. The predation rate increases because at the same time the per capita search rate decreases 3-fold, the number of small VBC increases 10-fold. Predators search progressively less area but find more VBC because the 10-fold increase in small VBC number offsets the 3-fold decrease in the search rate.

Region II of the model also can be explained in terms of the relative changes in the leaf area and small VBC. For example, between 10 and 20 VBC, there is a 2-fold increase in small VBC number. The amount of leaf area searched at 10 small VBC per 35,000 cm^2 leaf area is 1468 cm^2; at 20 small VBC, a predator will search 653 cm^2. Proportionally, the predator searched 0.042 of the 35,000 cm^2 for 10 small VBC, while at 20 small VBC, the predator searches 0.019 of the leaf area. While the number of small VBC increases 2-fold, the area searched decreases approximately 2.5-fold (.019/.042). This results in a decrease

in the number of small VBC attacked as the number of small VBC increased.

Region III of model behavior begins at approximately 24 small VBC and continues to 50 small VBC. Increases in small VBC result in more attacks, approaching a linear relation at 34 small VBC numbers. Predation increases in this region because at these high densities predators approach the minimum search rate of 400 cm^2. The 400 cm^2 searched represents approximately 1.1% of the total 35,000 cm^2 leaf area searched or, with respect to the number of small VBC present, 0.01 times the number present will be encountered and attacked. The 0.01 represents the slope of the line describing predation as a function of the number of small VBC (greater than 24) per 35,000 cm^2 of leaf area. Note that the numbers of small VBC per cm^2 leaf area in Region III exceed the densities found in the present study. Predator behavior at such high densities cannot, therefore, be verified with data from the present study. If the number of small VBC reach high enough levels, either predator satiation or handling time would then limit the number of attacks (Holling 1959, 1966).

There is close similarity between the form of the present description (especially in Region I) and the Holling (1959) functional response. In the Holling (1959) description, predation levels reach a plateau due to handling time limitations or due to predator satiation. For the range of numbers of small VBC per cm^2 leaf area,

in the present study, the rate of predation does not level off due to handling times or satiation. Predators catch so few prey, approximately one per 2.5 days, that the impact of handling time or satiation is clearly negligible. The ability of the predator to find prey in the extensive searching universe determined the number of attacks. Consumption behaviors and handling times apparently do not significantly influence predation on small VBC in soybean.

The form of the functional response is interesting when small VBC numbers reach very high levels. Here the predator exhibits a classic Type I response (Holling 1959)--what Collins (1980) found in his study of predation on small VBC. Note that the predator exhibits different types of functional responses depending on the number of small VBC. At low numbers of small VBC, a Type II response is indicated (Region I). At intermediate numbers of small VBC (Region II), a negative slope response is seen. At very high numbers of small VBC (Region III), a Type I response is evident. These results suggest that describing the response of a predator to prey density changes depends on the prey density over which the response is measured.

Leaf area. Shown in Figure 6.7 are the changes in the predation rate as the leaf area is increased from 5,000 to 80,000 cm^2. Again, the nominal predation rate at 35,000 cm^2 is indicated by a solid circle. As was seen in Figure 6.6, there are three distinct regions of model behavior.

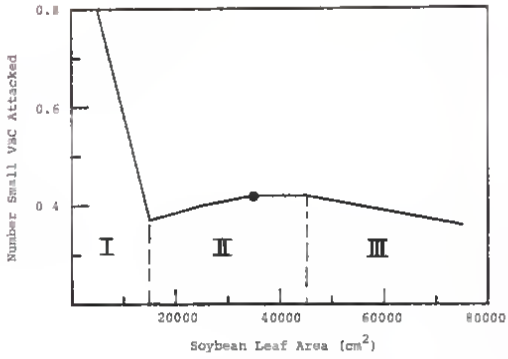

Figure 6.7. Per capita predation rate as a function of the soybean leaf area. Nominal value indicated by solid circle. Small VBC and predator number held constant.

Region I in Figure 6.7 shows a linear decrease in the predation rate as leaf area increases from 5,000 to 15,000 cm^2. In Region II, the predation rate increases as leaf area increases from 15,000 to 45,000 cm^2. In Region III, the predation rate again declines at leaf areas greater than 45,000 cm^2.

The three regions of model behavior correspond to the three behavioral regions shown in Figure 6.6. Region I of Figure 6.7 corresponds to the linear changes in predation in Figure 6.6 when the number of small VBC per cm^2 leaf area is high. In Figure 6.6, the number of VBC was increasing; thus, the slope was positive. In Figure 6.7, the leaf area is increasing, therefore, the predation rate decreases, and the slope is negative. Region II of Figure 6.7 corresponds to the decrease in predation seen in the Region II of Figure 6.6. Leaf area increases (which correspond to decreases in VBC number in Figure 6.6) result in predation rate increases because of the relative changes in searching area and the number of VBC encountered (see page 117). Region III in Figure 6.7 corresponds to the initial increase in predation seen in Figure 6.6 (Region I) at small VBC numbers less than 10. Again, the relative changes in VBC number and searching area results in the observed behavior in these regions.

The predation rate on small VBC in soybeans is dependent on four components: the number of predators, the number of small VBC, the amount of soybean leaf area, and

predator searching behavior. Predation dynamics are defined in terms of changes in these four components. A simple relation exists between the predation rate and the number of predators. As the number of predators increases, the predation rate increases linearly. However, for small VBC or leaf area changes, predation dynamics are more complex. The change in the predation rate depends on the relative magnitude of the change in either the leaf area or the number of small VBC. The description of the predation rate is also effected by the value of the C_i parameters in the predation model. To investigate the relative impact of changes in the value of the C_i parameters, parametric sensitivity analyses (see Overton 1977) were conducted. The results of those analyses are presented in the next section of this chapter.

Parametric Sensitivity Analyses

The parameters C_1, C_2, and C_3 represent ecologically relevant factors describing the per capita search rate as a function of the number of small VBC per cm^2 leaf area. The parameter C_3 (= 400 cm^2) represents the minimal area searched by a predator in a 24 hour period. The C_1 parameter (= 4515 cm^2) represents the maximal increase in the area searched when the numbers of small VBC per cm^2 leaf area equals zero. The parameter C_2 (= 5045 cm^2/number of small VBC) represents the magnitude of the changes in

searching as the number of small VBC per cm^2 leaf area changes. The C_2 parameter can be thought of as a measure of the rate of change in searching as a function of the number of small VBC per cm^2 leaf area (the larger the value of C_2 the "faster" the rate of descent to C_3).

The focus of the sensitivity analyses was to determine the relative contribution of each parameter to the changes in the rate of predation on small VBC in soybeans. To judge the relative contribution for each C_i parameter, the standard value of each parameter was independently increased or decreased 10%. Numbers of small VBC per cm^2 leaf area varied from 0.00 to 0.0007, a realistic range of small VBC densities in the field. Changes in the predation rate as a function of the changes in the value of specific C_i parameters were then compared to standard predation values and to the magnitude of changes seen when the other C_i parameters were altered. The parameter which causes the largest change in the predation rates is the parameter to which the model is most sensitive.

Results of the parametric sensitivity analyses are displayed in Figures 6.8. Standard runs are indicated by solid lines. The -10% changes are indicated by dotted lines and the +10% changes by the dashed lines. Figure 6.8a shows the predation rates given changes in the C_1 parameter, 6.8b for C_2, and 6.8c for C_3, respectively. The analyses indicates for 10% parametric changes in the values of the C_i parameters, the model is more sensitive to the

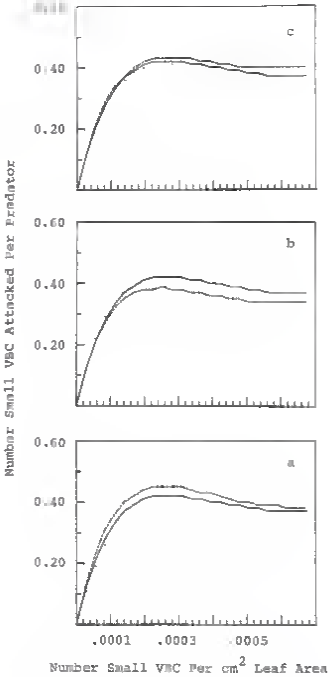

Figure 6.8. Per capita predation rate for standard (solid lines) +10% (dashed lines) and -10% (dotted lines) values of C_i. Parameter C_1 (a), parameter C_2 (b), and parameter C_3 (c).

rate of change in per capita search (C_2) than to minimal (C_3) or maximal (C_1) search rates. It is interesting to note that regardless of which parameter is changed, the level of predation remains remarkably consistent. When the number of small VBC exceeds 0.0001% per cm^2 leaf area, a predator attacks approximately 0.4 small VBC with only minor variation for the 10% parametric changes. This result is another indication of the formidable task facing searching predators in the soybean system. The relative stability of the model given 10% parametric changes indicates that much higher parametric changes would be necessary to significantly affect the per capita predation rate.

A Model of Small VBC Dynamics in Soybean

The impact of predation on small VBC dynamics will vary as the number of predators, small VBC, and leaf area changes. Because predation of small VBC in soybeans is such a dynamic process, detailing predation in the soybean system requires suitable model structure that incorporates descriptions of VBC, predator populations, and leaf area changes. Described below is a model that couples small VBC, predator, and leaf area dynamics. The temporal and spatial resolution of this dynamics model is 24 hours and 91 cm of soybean row, respectively. The effect of changes in leaf area, small VBC, and predator growth rates will be investigated specifically by systematically altering

parameters describing leaf area, small VBC, and predator dynamics. The objective of this approach is to (1) describe plausible scenarios of small VBC, predator, and leaf area dynamics and (2) to investigate predation under a range of realistic field conditions. The intent of the following section is not to present a validated mechanistic soybean crop system model but to show how predation influences small VBC dynamics in soybean and to indicate how changes in the soybean system specifically influence predation.

Dynamics Model Development

Leaf area sub-model. Net changes in soybean leaf area are the result of leaf area increases due to soybean plant utilization of environmental resources and of the negative impacts of defoliation, senescence, and pathology. The Soybean Integrated Crop Management (SICM) model (Wilkerson et al. 1983) has a detailed mechanistic description of soybean growth which shows that soybean leaf area growth follows a relatively consistent pattern. This pattern of leaf area growth can be described in terms of distinct growth intervals. Following preliminary emergence and plant growth, there is an interval of linear leaf area growth followed by a plateau where the plant maintains essentially a constant leaf area. Following this plateau region is an interval of linear leaf area decline followed by an interval of exponential leaf drop and leaf senescence at the end of the season.

The SICM model can be used to estimate the slopes and durations of each growth stage over a variety of weather patterns. Curves of leaf area dynamics can be obtained and estimates of the slopes and stage intervals can then be averaged over a variety of conditions to obtain mean values for use in describing a general model of leaf area dynamics (see Table 6.5). Equations describing leaf area growth during each stage interval were written and translated into Fortran IV (Cress et al. 1970) and programmed into a digital computer (Digital Corporation PDP® 11/23 computer). A copy of the program, including all sub-model descriptions is given in Appendix D. The general form of the leaf area sub-model is given by:

$$A_{t+1} = A_t + \Delta A_t \qquad 6.6$$

where;

A_t = leaf area in cm^2 (both leaf sides) at time t

ΔA_t = daily change in leaf area.

Inserting expressions for ΔA_t for growth intervals exhibited by soybean (Table 6.5) allows description of the changes in leaf area thru time. The equations governing leaf area growth are shown in Appendix D.

Small VBC sub-model. VBC population changes are the net results of various inputs (births and immigration) and

Table 6.5. Leaf area growth parameters estimated from simulation of the SICM model for Gainesville, Florida.

Year	Initial leaf area (cm^2)	Daily growth rate (cm^2)	Duration (days)	Maximum leaf area (cm^2)	Duration (days)	Daily decline rate (cm^2)	Duration (days)
1978[a]	14000	2143	28	74000	16	-400	60
1979	4500	1066	38	45000	10	-423	52
1980	5000	1053	38	45000	16	-546	55
1981	5000	1061	33	40000	12	-394	66
1982	10000	1741	28	58000	12	-434	53
Average	7700	1408	33	52400	13	-439	57

[a]Estimates for Quincy, Florida

outputs (deaths and emmigretion) Mathematically, small VBC dynamics can be expressed as

$$V_{t+1} = V_t + I_V + rV_t - N_a - dV_t - bV_t \qquad 6.7$$

where;

V_t = the number of small VBC at time t

I_V = the net influx rate of small VBC into the system in numbers per day from non-resident adult VBC immigration

r = daily population growth rate of small VBC

N_a = number of small VBC consumed by predators (see Equation 6.4)

d = daily proportion disease mortality rate of small VBC

b = daily proporetional background mortality rate of small VBC

Values for I_V and r were arrived at by serially inserting unique sets of I_V, r values into a preliminary small VBC dynamics sub-model and comparing the sub-model output with a generalized description of small VBC population changes Thus, parameters were not adjusted such that the sub-model specifically "fit" a particular data set but such that the sub-model would describe the general pattern of small VBC dynamics exhibited in Figures 5.1 and 5.2. Influxes of small VBC were set to begin after Julian day 215 (August 3) when, according to sampling data (Appendix

A), at least one small VBC per 91 cm of soybean row was first found. The daily background mortality rate (b) is set at 0.15, a value within the range of background mortality found in previous studies (Collins 1980, Elvin 1983).

The final component of the small VBC sub-model describes the influence of Nomuraea rileyi epizootics. As discussed previously (see Chapter II), epizootics of N. rileyi can decimate high density VBC populations. Anderson and May (1980) have detailed the general characteristics and modeled host/pathogen interactions, like that seen with VBC and N. rileyi. Epizootics usually occur when host populations are dense and abiotic environmental conditions are conducive to pathogen outbreak. By examining sampling data (see Appendix A), N. rileyi epizootics were estimated to begin shortly after Julian day 244 (September 1) and when the number small VBC per cm^2 leaf area exceeded 0.000275. By serially inserting values of "d" into a preliminary small VBC dynamics sub-model and comparing sub-model output with a generalized description of small VBC population changes, a value of 0.15 was derived for the parameter d. As with leaf area and small VBC parameters, the N. rileyi component is not intended to be a mechanistic description of host/pathogen interactions. The N. rileyi component serves to rapidly decrease VBC population densities late in the season as is seen in the field data (see Figures 5.1 and 5.2).

The final form of the small VBC sub-model with parameter values inserted is given by.

$$V_{t+1} = V_t + 1.0 + 0.175V_t - N_a - 0.15V_t \qquad 6.8$$

when $t \geq 215$, and:

$$V_{t+1} = V_t + 1.0 + 0.175V_t - N_a - 0.15V_t - 0.15V_t \qquad 6.9$$

when $t \geq 244$ and the number of small VBC per cm^2 leaf area ≥ 0.000295.

Predator sub-model. Sampling data showed that predator populations quickly attain and then maintain a population density of approximately one to three predators per 91 cm of soybean row (see Appendix A and Figures 5.1 and 5.2). In the present description, predator population dynamics was assumed to be a function of four components: (1) net predator consumption rates, (2) conversion of attacked small VBC into predator offspring, (3) predator deaths, and (4) predator net immigration rates. Except for the present predator model (Equation 6.4), no data exists concerning these components. Therefore, the predator sub-model will be described and parameters estimated such that the sub-model generally describes predator population dynamics seen in sampling data. The general form of the predator sub-model is given by:

$$P_{t+1} = P_t + aN_a + I_p - mP_t \qquad 6.10$$

where;

P_t = number of predators at time t

s = conversion rate for ingested small VBC numbers to predator offspring

N_s = number of small VBC attacked (see Equation 6.4)

I_p = predator net immigration rate

m = daily proportional mortality rate of predators.

The values of s, m, and I_p were estimated as were the small VBC parameters by inserting values for each predator parameter into a preliminary sub-model until a satisfactory fit to a generalized description of predator dynamics was obtained. Inserting the values of the parameters into Equation 6.10 gives:

$$P_{t+1} = P_t + .05N_s + .40 - .05P_t \qquad 6.11$$

Thus, predators convert 5% of attacked small VBC into predator offspring; 0.40 predators daily immigrate into 91 cm of soybean row, and 5% of the predators die daily.

Dynamics Model Behavior

Shown in Figures 6.9 and 6.10 are the number of small VBC and predators and the leaf area predicted by the dynamics model, respectively. Comparing Figure 6.9 with Figures 5.1 and 5.2 shows that the model adequately captures the nature and dynamics of both small VBC and predator population dynamics in soybean. Comparison of Figure 6.10

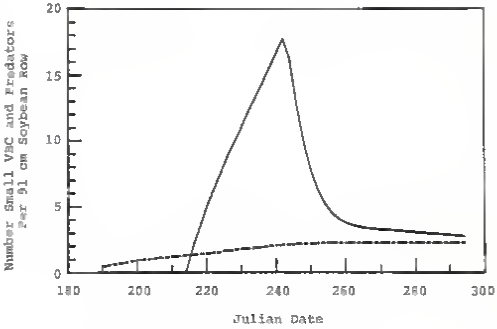

Figure 6.9 Number of small VBC (solid line) and predators (dashed line) per 91 cm of soybean row as predicted by the VBC dynamics model.

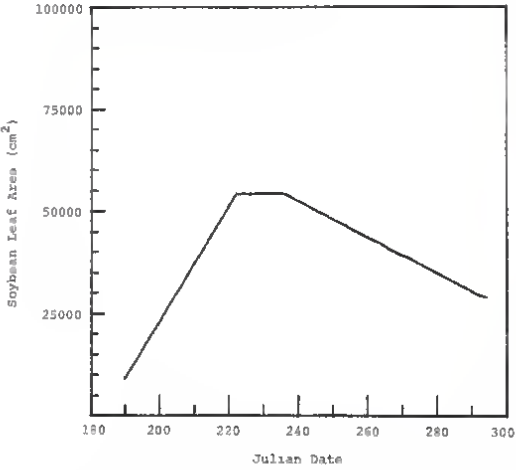

Figure 6-10. Soybean leaf area (cm^2) per 91 cm of soybean row as predicted by the VEC dynamics model

with Figures 5.4 and 5.5 shows that the model also adequately describes leaf area dynamics in this system. The dynamics model is, therefore, judged to be an adequate representation of the behavior of the components of the soybean system which most influence predation. The objective in developing the dynamics model was to investigate the impact of predation, VBC life history, and leaf area changes on small VBC population dynamics.

Dynamics Model Analyses

The strategy for model analyses involved investigation of the impact of small VBC and predator population and the leaf area changes on small VBC dynamics in soybean. To implement realistic field changes in small VBC and predator number or leaf area, one parameter from each sub-model was selected for independent manipulation. To invoke leaf area changes, the leaf area growth rate during the linear growth interval (GROLF = 1408 cm^2 per day; see Appendix D) was selected. Different VBC scenarios were developed by manipulating the small VBC population growth rate (r = 0.175). Predator population changes were effected by altering the conversion rate of small VBC to predator offspring (e = 0.05). Note that the present analyses focus on determining how small VBC, predator, and leaf area changes effect small VBC dynamics. What causes the change in small VBC, predators, or leaf area is not germane here.

For example, in the present analyses, predator population growth was changed by altering the small VBC-to-predator conversion rate (a). Changes in predator number could have been obtained by altering the predator death rate (m). Similar comments apply to small VBC and leaf area changes.

The relative values of the modified parameters will be hereafter referred to as the "standard," "low," and "high" values. The standard, low, and high values for the small VBC population growth parameter (r) are 0.175, 0.150, and 0.200, respectively. The standard, low, and high leaf area linear growth parameter (GROLF) values are 1400, 1300, and 1500, respectively. The standard, low, and high predation parameter (a) values are 0.05, 0.01, and 0.10, respectively. Since there were three parameters each with three values, there were a total of 27 possible independent scenarios or modal simulations.

Results of the simulations are shown in Figures 6.11 to 6.13. Figure 6.11 depicts the small VBC dynamics for low (Figure 6.11a), standard (Figure 6.11b), and high (Figure 6.11c) leaf area regimes. For all curves in Figure 6.11, the small VBC population growth rate was set at the standard value (r = 0.175). Solid lines in Figure 6.11 represent standard predator regimes. Dotted and dashed lines of Figure 6.11 are for high and low predation regimes, respectively.

Figure 6.12 represents the small VBC population growth for low (6.12a), standard (6.12b), and high (6.12c) leaf

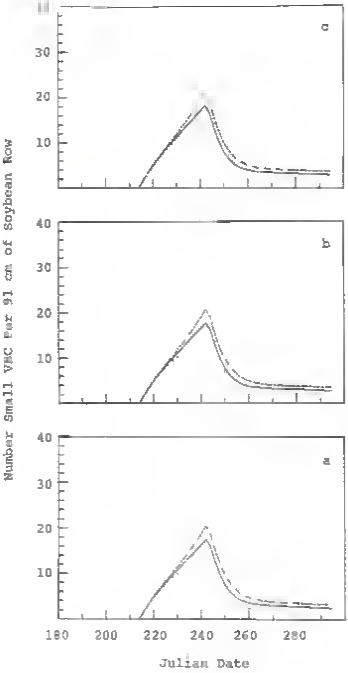

Figure 6.11 Number of small VBC per 91 cm of soybean row for standard VBC population growth under low (a), standard (b), and high (c) leaf area regimes. Standard predator (solid lines), low predator (dashed lines), and high (dotted lines) conversion rates.

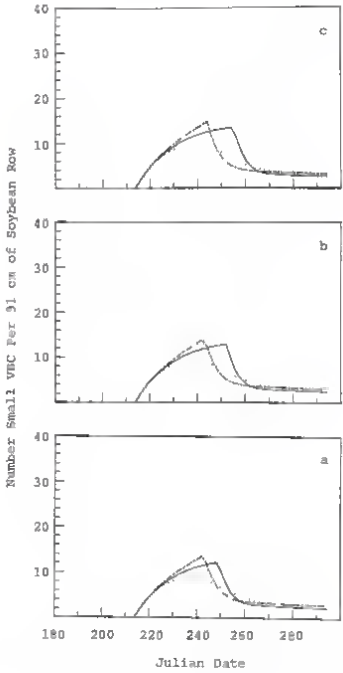

Figure 6.12 Number of small VBC per 91 cm of soybean row for low VBC population growth under low (a), standard (b), and high (c) leaf area regimes Standard predator (solid lines), low predator (dashed lines), and high (dotted lines) conversion rates.

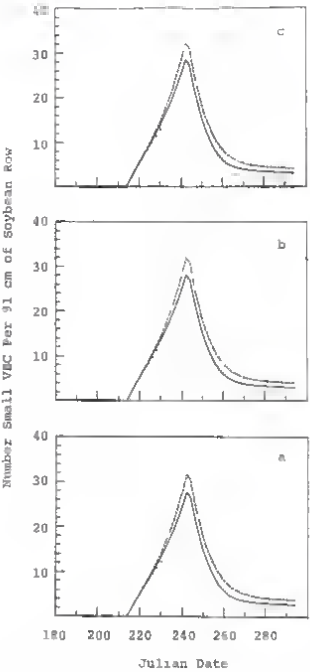

Figure 5-13. Number of small VBC per 91 cm of soybean row for high VBC population growth under low (a), standard (b), and high (c) leaf area regimes-Standard predator (solid lines), low predator (dashed lines), and high (dotted lines) conversion rates

area regimes. The small VBC population growth rate for all curves in Figure 6.12 was set at the "low" value (r = 0.15). The solid, dotted, and dashed curves shown in Figure 6.12 represent the small VBC population growth given standard, high, and low predator populations, respectively.

Finally, Figure 6.13 shows the small VBC population growth for three leaf area regimes [standard (a), low (b), and high (c)] given standard (solid lines), low (dashed), and high (dotted) predator populations, respectively. For all curves in Figure 6.13, the small VBC population growth rate was set at the high value (r = 0.20).

When the small VBC population growth rate is at a standard value (Figure 6.11), small VBC densities, over the range of leaf area and predator regimes, follow a characteristic pattern. Peak small VBC populations are reached around Julian day 240. Higher predator populations decreases the magnitude of the small VBC peak densities (compare solid, dashed, and dotted lines), however, in general, standard small VBC population growth results in approximately 12 to 22 small VBC per 91 cm of soybean row at peak densities depending on the predation pressures.

At a low small VBC population growth rate (Figure 6.12), overall small VBC population densities are lowered. Small VBC populations reach peak densities around Julian day 240, although the temporal range here is greater than that seen in Figure 6.11. Again, predators lower the growth curves, the magnitude being a function of predator

densities. The range of peak small VBC population densities (per 91 cm of row) is between 8 and 14 small VBC larvae.

At a high small VBC population growth (Figure 6.12), small VBC densities reach higher densities than witnessed in either Figures 6.11 or 6.12. Again, higher predator populations lead to lower small VBC densities (compare dotted, dashed, and solid lines). Small VBC densities peak around Julian day 240, with a smaller temporal range than seen previously. The range of peak small VBC densities are between 20 to 35 per 91 cm of soybean row.

The simulations clearly indicate that higher predator densities will lead to lower small VBC densities as to be expected. More predators present will lead to more small VBC being attacked; thus, the population density of small VBC would be expected to be lowered in the higher predator regimes.

The key finding of these analyses is the determination of the relative impact of VBC life history and soybean leaf area changes. Within each of Figures 6.11, 6.12 and 6.13, leaf area changes while VBC population growth rate is held constant. Note that regardless of the leaf area changes, the same densities of VBC are attained (compare graphs a, b, and c within any figure). Examination of the densities of VBC when the leaf area is constant and the small VBC growth rate changes (compare Figures 6.11a, 6.12a, 6.13a, etc.) clearly shows the impact of changes in the small VBC growth

rate. At low leaf area regimes (Figures 6.11a, 6.12a, and 6.13a), small VBC densities increase as small VBC growth rates increase. Comparison of small VBC densities over standard leaf area regimes (Figures 6.11b, 6.12b, or 6.13b) shows a similar trend--increase in small VBC density as the small VBC growth rate increases. At high leaf area regimes (Figures 6.11c, 6.12c, and 6.13c), small VBC densities also increase as the small VBC growth rate increases.

Results indicate that predators are able to compensate for leaf area changes but are unable to compensate for VBC reproductive changes. The model, therefore, indicates that the key determinants of small VBC dynamics in soybean are (1) the small VBC growth rate and (2) the predator population densities. Leaf area changes are not determinants of small VBC densities per se because predators can compensate for leaf area changes. The density of small VBC in soybean fields is, therefore, primarily a function of small VBC and predator interactions. While predators apparently compensate for leaf area changes, evidently they are unable to compensate for small VBC growth rate changes.

The model is consistent with previous views of the role of predators in VBC dynamics in soybean (J.L. Stimac[3] personal communication). In general, predators were viewed as important factors of low density, endemic VBC population dynamics. As VBC immigration, reproduction, and/or developmental rates increase, predators were unable to respond adequately to dampen VBC density increases. The lack of a

significant predator numerical response was viewed as contributing to the ineffectiveness of predators at controlling high density VBC populations. The present study provides experimental, analytical, and theoretical arguments that augment and establish the ecological reasons for predator behavior in this system.

Notes

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[2]Elvin hypothesizes that more accurate estimation of predation on small VBC in the soybean foliage is given by "predator induced" mortality estimates [see Elvin (1983)]. Comparison of modal predictions versus "predator induced" mortality shows that for 15 of 20 possible comparisons (1981, 1982), the model predicts the estimated mortality to within one small VBC attacked. The temporal dynamics of the modal and the estimated mortality were similar for 16 of 19 possible comparisons.

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CHAPTER VII
SUMMARY AND CONCLUSIONS

Introduction

In this chapter, the findings and implications of the present study are summarized and discussed. A brief summary of the important components of arthropod predation on small VBC in soybean will be presented. The nature and influence of the functional and numerical responses (Solomon 1949) of arthropod predators in the soybean system will be discussed, and how the present study relates to predation in other systems will be described. The chapter closes with a discussion of the major conclusions to be drawn from this study and suggested research avenues that are evident from this study of arthropod predation in the soybean system.

Summary of Predation in Soybean

Predation on small VBC larvae in soybean was shown to be a function of the number of small VBC, the number of predators, soybean leaf area, and the predator searching behavior. The soybean leaf area defines the searching universe and together with the number small VBC determines the probability of encounters between predators and prey

The low probability of encounter (maximum of 0.00067 per cm^2 of leaf area searched (see Tables 5.1 and 5.2) means that a predator must search considerable leaf area to find a small VBC. The per capita predation rate of one small VBC every 2.5 days is a clear indication of the immensity of the task facing searching predators.

The present research emphasizes that the dynamic nature of the soybean system, specifically the relative changes in the leaf area and numbers of small VBC, dictates the limits of predation in this system. Predators unable to maintain an adequate search rate or predators that expend too much energy searching will not be found attacking small VBC or other prey items over an extended time period. Therefore, predators consistently found in soybean are either those predators that search the soybean leaf area and find prey or are predators that are unaffected by leaf area changes.

The nine predator species used in the present study (see Table 4.1) are consistently found in soybean (see Chapter IV). Logically, these predators can find prey in the soybean canopy. That there was no demonstrable relationship between the species composition of the predator complexes and the predation rates indicates that something other than predator species composition determines the level of predation of small VBC in soybean. This is not to say that the species are 'unimportant' to predation in soybeans. Each species is adapted to search the soybean leaf

area, therefore, changes in the species composition of predator complexes are 'self compensating'. That is, small VBC not attacked by predator species A are available for attack by predator species B. Since both species A and B can find prey in the soybean canopy, the specific identity of predators is not as critical to predation as is the number of predators present. Because the system defines the 'type' of predators that will consistently find prey in soybeans, a self compensating mechanism exists. Predation may, therefore, be described more in terms of predator number than in species composition of the predator complexes.

Excepting pupae, all VBC immature stages are found on soybean foliage. To some extent, predators are VBC stage or size-specific (Elvin 1983). The location of VBC immatures in the foliage presents the same searching problems to predators, large amounts of area must be searched to find prey. Therefore, remarks on predation of small VBC undoubtably apply to predation on other VBC immature stages found in the soybean foliage. With parametric modification, the predation model (Equation 6.4) could be used to describe predation on other VBC immature stages.

Predator Functional Response

Solomon (1949) defined the predator functional response in terms of the changes in the number of prey attacked as a function of prey density. Holling (1959, 1961) detailed

three general types of responses (Figure 3.1) and provided the behavioral rationale behind the functional responses. Essentially, the form of the predator functional response is due to the effects of handling time and predator satiation. Predators must spend time capturing, consuming, and processing prey. The more prey captured the less time available to search for other prey. As prey density increases, predator efficiency declines. Satiation has a similar effect on the functional response. As predators become satiated, searching and capture rates decline.

In the present study, predators showed a functional response to the number of small VBC per cm^2 leaf area. When the behavior of the predation model was examined (Figure 6.6), the nature of the functional response changed depending on the number small VBC per cm^2 leaf area. When the per capita predation rate was plotted as a function of the number small VBC per cm^2 leaf area inside the cages (Figure 5.22), the rate of predation was shown to be fairly consistent; indicating that the predation rate was at or near the plateau region of the functional response curve. While not surprising that predators show a functional response to prey density, the mechanism for the functional response was found to be different from those previously postulated (see Holling 1959, 1965, Hassell 1978)

In the present study, constraints of handling times or satiation did not determine the number of small VBC attacked by predators. Predator searching behavior determined the

functional response. When the number small VSC per cm^2 leaf area was low, predators searched considerable amounts of leaf area; they must to find prey. As number small VSC per cm^2 leaf area increased the search rate decreased (Figure 6.1). When the number small VSC per cm^2 leaf area was high, predators do not need to search as much leaf area to find prey. Why predators did not maintain high search rates when the number small VSC per cm^2 leaf area was high was probably a function of two limitations, time and energy.

Predators searching for prey are not conducting other activities such as ovipositing, mating, or resting. In addition, since predators themselves have natural enemies (Richman et al. 1980), time spent searching for prey exposes the predators to attack. The larger the amount of time searching, the higher the probability of being attacked by other predators.

Searching large amounts of leaf area also required an investment in energy. The more area searched, the more energy expended. The energy costs of searching must be offset by the energy benefits of capturing prey. If the cost/benefit ratio of a high search rate does not exceed the cost/benefit ratio of a variable (conservative) search rate, then there is no energetic reason to maintain the higher search rate (Odum 1983).

Finally, studies have consistently shown (e.g., see Murdie and Hazzell 1973) that when a predator perceives the presence of prey, searching behavior changes.

Characteristically, the predator executes a series of tight circles that keep the predator in the region of the prey, increasing the probability of finding neighboring prey (Hassell 1978). In the present study, when the number small VHC per cm^2 leaf area was high, predators search less area. Perhaps having contacted prey, the predators in the present study limit search to the immediate area. The predators localize their search to find other nearby prey. When searching is estimated as a function of the proportional attack rate and the total leaf area, localized predator search would appear as a low search rate. What appears to be an inefficient searching behavior may be the result of localized searching at high density patches. The predator search rate (Figure 6.1) may reflect a prey exploitation strategy such that after contact with prey, localized searching begins.

Predator Numerical Response

Solomon (1949) defined the change in predator number as a function of prey density to be the numerical response. Increases in the number of predators is achieved through two basic processes, either higher reproduction or (net) immigration rates (Hassell 1978). The increase in the number of attacks by a predator functional response can lead to higher rates or reproduction as more food items are consumed at higher prey densities. There need not be a 1:1

correspondence between the increase in the attack rate and changes in reproduction (Holling 1961).

The second driving factor of the numerical response is increased immigration and predator aggregation at high prey densities (Beddington et al. 1978). Locally, dense concentrations of prey are attractive to predators which leads to increases in predator number in these sites. With both the reproductively and migrationally driven numerical response, there is often a time lag between increases in prey density and the changes in predator density.

In the present study, changes in predator density showed no relationship between either changes in the number of small VBC per 91 cm of soybean row (Figures 5.1, 5.2, and 5.3) or the number small VBC per cm^2 leaf area (Figures 5.16 and 5.17). Predators were seen to quickly attain and then maintain an equilibrium density in both years of the study. The predators showed no numerical response to small VBC density changes.

There were probably two reasons for the lack of a numerical response by predators in the soybean system. First, predators were shown to have an essentially constant attack rate (Figures 5.9 and 5.22). With a constant input of prey biomass, predators had no increased food reserves to 'fuel' increased reproduction. While the predators undoubtably supplement their diet with alternative prey (including plant sources), apparently the level of

predation from all sources was too low to catalyze the numerical response.

Secondly, evidence for the lack of a predator numerical response (see Figure 5.3) indicates that the predators do not increase colonization rates into soybean fields in response to increases in VBC density. Whatever the colonization rate of predators into soybean, VBC density does not have an appreciable effect. Whether the predators are unable to perceive the changes that do occur in small VBC densities or the changes in small VBC density are too low to trigger predator behavioral changes cannot be addressed here.

Impact of Predation in Soybean

Functional and numerical response of the predators to changes in prey densities constitute the total response of the predator population (Solomon 1949, Holling 1961, Huffaker et al. 1976). In soybean, while a Type II functional response was indicated (Figure 6.2), the predators attack essentially a constant number of small VBC over all small VBC densities (Figures 5.9 and 5.22). Similarly, the numerical response was shown to be insignificant. There is approximately a constant number of predators attacking small VBC over all small VBC densities (Figure 5.3). The net result of the functional and numerical responses of predators is that the predation rate is remarkably constant

through time. A constant number of small VBC are attacked regardless of the number of small VBC present. At low densities of small VBC, predators will have a significant impact and could prevent VBC outbreaks. If VBC reproduction, immigration, or developmental rates increase, then predators will be unable to contain VBC population growth. Given observed VBC dynamics (Figures 5.1 and 5.2), predators do not control VBC populations.

By taking a constant number of small VBC, predators are behaving in accordance with the economic analogy of Fimmental et al. (1963). According to those workers, predators attack the 'interest' of prey populations, leaving the principle alone. As in economics, removing only the interest will not decrease the amount of principle. In the soybean system, predators only remove the VBC 'interest' and leave the VBC principle to increase.

Predators attack the excess number of small VBC, the VBC 'interest.' We can see ancillary evidence for the nature of predation by examination of Figures 5.16 and 5.17. Figures 5.16 and 5.17 show the field VBC density expressed in terms of numbers per 91 cm of soybean row and numbers per cm^2 leaf area for 1981 and 1982, respectively. Note the close similarity between the curves for both types of densities. Since leaf area changes are not synchronized with small VBC number changes, there should be no a priori reason to expect the curves to appear similar in shape (contrast Figures 5.16 and 5.17 with Figures 5.18 and 5.19)

If, however, some mechanism exists for removing the excess number of small VBC larvae as a function of leaf area, then similar curves for the number of small VBC per 91 cm of soybean row and on a per cm^2 leaf area basis are to be expected. It is the cropping of excess numbers of small VBC by predators which results in the observed similarity in the curves of Figures 5.16 and 5.17.

Conclusions

The velvetbean caterpillar has been the object of extensive study (see Ford et al. 1975). The basic components of VBC dynamics have been detailed (see Neal 1974, Moscardi 1980, Elvin 1983) and mathematical models of VBC dynamics described (e.g., Wilkerson et al. 1983). Finally, the conceptual framework of VBC dynamics in soybean has been identified (Stimac and Barfield 1980). The present research has clearly shown that understanding the dynamics of a given process requires a systems perspective. Critical to the description of an ecological process is the interpretation of selected behaviors in the context of system dynamics (see Stimac 1981). Classical functional response analyses, conducted in high density laboratory situations (see Hassell 1978 for examples), point to the influence of predator feeding behaviors on predation. The present study conducted under field conditions showed the overriding influence of searching behavior on predation. While searching

behavior has been previously identified as a key element in predation (Smith 1939, Ullyett 1943, 1949b, Burnett 1958b, DeBach 1964, 1974, Huffaker et al. 1976, Risch et al. 1982), classical functional response research has emphasized consumption. The need for future research on the impact of searching behavior on the functional response is clearly indicated by the demonstrated importance of searching on predation dynamics.

Suggested Research Avenues and Applications

The present research described predation as a function of the changes in the soybean system. The analyses of the dynamics model (Figures 6.11 to 6.13) showed the relative importance of characteristic changes in these soybean system components. Assuming that predation on other VBC immature stages follow similar patterns, the following research avenues and applications are suggested.

As shown previously, changes in the leaf area do not significantly effect VBC dynamics. Predators are able to compensate for leaf area changes. While more research is needed, the predator/leaf area relationship suggests that attempts at managing VBC populations by cultivating smaller soybean plants will be largely unsuccessful. Predators compensate for leaf area changes by searching differing amounts of leaf area. As leaf area decreases, the number of VBC per cm^2 leaf area increases. The predators respond

to increases in the number of VBC per cm^2 leaf area by searching less area. The net result is a constant attack rate. The same impact of predators on VBC dynamics would be expressed on smaller soybean plants. Smaller plants would have the additional debit of being more sensitive to leaf loss from herbivores like VBC (see Luna 1979).

The dynamics model analysis clearly indicated that changes in VBC reproduction had a significant impact on VBC dynamics. The analyses examined only the effect of reproductive changes, but changes in VBC migration or developmental rates would have similar effects. Basic research is needed to determine how VBC reproduction, migration, or developmental rates change. Specific research is needed to clarify the impact of alternative host plants on VBC reproduction, to describe the timing and magnitude of adult VBC migration, and to describe the changes in VBC survivorship, including predation on other VBC stages. Research needs to be focused on the measurement of VBC reproduction, migration, and development under field conditions. To analyze the importance of various components of VBC dynamics, a suitable framework is necessary. The SICM model (Wilkerson et al. 1983) could provide the necessary framework if mechanistically driven sub-models of VBC dynamics are described. Only in the context of the soybean system dynamics will VBC life history be properly characterized.

The dynamics model analyses also suggested that VBC dynamics can be affected significantly by increases in

predator density. An increased number of predators leads to higher predation thereby decreasing VBC numbers. In a practical sense, several methods have been suggested to increase the level of predation including: augmenting existing predator population (Rabb et al. 1976), providing predators with alternative prey resources (van den Bosch et al. 1976), providing alternative predator habitats (Altierri 1979), and introducing new predator species (DeBach 1964).

Changes in the number of predators through time indicates that what food resources found in and around soybean are not sufficient to sustain a numerical response. Neither the increase in predator reproduction nor migration rates leads to the increases in predators necessary to offset increases in VBC number. Adding additional predators (of the same species) either through augmentation or by providing alternative prey items or habitats will be unsuccessful unless there is enough total prey available to increase the predators numerical response. While temporarily increasing the number of predators, augmenting the numbers of predators does nothing to increase the number of available prey or alter predator searching behaviors. There would be no a priori guarantee that the released predators would remain in or around soybean fields. Alternatively, increasing prey of habitat heterogeneity will not change the basic behavior of predators. Predators would still have to find prey by searching less area, and unless the

combined number of alternative prey and VBC per cm^2 leaf area increase to very high levels, predator searching behavior would nullify most positive effects. Finally, increasing habitat heterogeneity may increase the total area predators of small VBC would have to search. This would lower the proportion of soybean leaf area searched (presumably where the VBC would be located) and, thus, the attack rate on VBC (see Riech et al. 1982). Only if habitat heterogeneity increased the total number of searching predators or increased the predator search rate in soybean could increases in predation on VBC be expected.

Introducing new species into agricultural systems to control pest species is an historically valid method of pest control (DeBach 1964). In the soybean system, any introduced species clearly should be a different 'type' than species presently endemic. Specifically, the new species should more efficiently search the soybean canopy and/or have lower energy requirements for reproduction and shorter generation time. Key to successfully maintaining VBC at acceptably low densities will be the ability of predators to find VBC in the soybean leaf area. The ability to find VBC in the searching universe may be related to the degree of host specificity of the predator species. Host specific ones would negate the influence of the leaf area on predator searching. Therefore, the most likely candidates for successfully maintaining VBC at acceptably low densities would be specific, short lived, predators (<u>seneu</u>

late). Long lived generalist predators would have a lower probability for success.

The study has shown the benefit of integrating field experimentation and model analyses. Without the proper structure (model), the nature and impact of predation in this system would not have been determined. Conversely, only because of the critical experimentation were the data available for model analyses. Together the model/experimental approach has yielded significant insight into the process of predation in soybean. This approach has also provided the experimental and theoretical framework for making practical (management) decisions--something sorely lacking in the applied literature (Barfield and O'Neil 1984).

Finally, the present study has allowed a view of predation within the context of the overall system. Few studies have examined predation as part of overall system dynamics (for examples see Hughes and Gilbert 1968, Baumertner et al. 1981). Predation is intimately tied to other components of the soybean system. Isolating predation in an attempt to determine the relative importance of predation to prey population dynamics will not present an accurate description of this complex ecological process.

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APPENDIX A
SAMPLING DATA

Table A.1. Mast cloth sampling data for 1981.

Julian date	Number samples	Average number				
		1	2	3	4	5
208	12	.08 (.29)	.17 (.39)	.00	.08 (.29)	.08 (.29)
210	20	.05 (.22)	.10 (.31)	.05 (.22)	.05 (.22)	.00
215	20	.45 (.61)	.05 (.22)	.15 (.34)	.00	.00
217	20	.25 (.55)	.10 (.31)	.05 (.22)	.00	.00
222	20	.50 (.69)	.05 (.22)	.20 (.41)	.05 (.22)	.00
224	20	.25 (.55)	.05 (.22)	.05 (.22)	.15 (.49)	.10 (.31)
229	20	.80 (.83)	.00	.25 (.44)	.10 (.31)	.05 (.22)
231	10	.10 (.32)	.10 (.32)	.20 (.42)	.00	.20 (.42)
236	20	.45 (.61)	.05 (.22)	.05 (.22)	.10 (.31)	.10 (.31)
238	10	1.00 (.82)	.00	.20 (.42)	.30 (.68)	.10 (.32)
241	10	.10 (.32)	.00	.30 (.48)	.40 (.70)	.00
245	15	.47 (.74)	.07 (.26)	.27 (.46)	.13 (.35)	.00
248	13	.77 (1.36)	.00	.08 (.28)	.15 (.38)	.08 (.28)
252	10	1.30 (1.77)	.00	.20 (.42)	.20 (.63)	.10 (.32)
255	10	.50 (.53)	.00	.10 (.32)	.20 (.42)	.10 (.32)

Table A.1--extended.

(SD)[a] of species[b]					Maximum number predators[c]	Number diseased small VBC[d]
6	7	8	9	10		
00	17 (.39)	08 (.29)	.00	.08 (29)	2	0
00	10 (.31)	.00	.00	.15 (34)	2	0
00	.05 (.22)	.00	.00	.00	2	0
.00	.05 (.22)	.15 (34)	.10 (31)	.00	2	0
.00	.00	.00	.05 (.22)	.10 (.31)	2	0
.00	.20 (62)	.30 (47)	.10 (.31)	1 00 (.92)	3	0
.05 (.22)	.05 (.22)	.00	00	2 30 (1 42)	3	0
.20 (.42)	.00	.60 (.70)	.10 (.32)	4.10 (2 85)	5	0
.10 (.31)	.10 (.31)	.00	.15 (.34)	4 25 (2 63)	3	0
.10 (.32)	00	.40 (.52)	.20 (63)	4.70 (1.77)	3	0
.20 (.42)	.10 (.32)	.20 (42)	.40 (.52)	4.10 (3 00)	4	0
00	.00	.27 (.46)	13 (.35)	10 00 (4 14)	4	0
.08 (28)	.08 (28)	.69 (86)	.15 (38)	11.62 (5.92)	5	10
00	00	.20 (42)	20 (63)	15 80 (7 35)	5	1
.00	.00	.70 (1.25)	10 (.32)	19 30 (10 59)		

Table A 1--continued

260	10	1.00 (1 89)	.00	.00	.00	.20 (42)
262	15	.73 (1 53)	.00	.11 (35)	.00	.00
266	10	.10 (.32)	.00	.10 (32)	.10 (32)	.10 (.32)
269	10	.70 (68)	.00	.40 (.52)	.10 (.32)	.20 (.42)
273	10	.90 (1.60)	.00	.20 (.42)	.00	.00

[a]Standard deviation.

[b]Species:
1 = Geocoris punctipes
2 = Geocoris uliginosus
3 = Trobiconabia capaiformia
4 = Nabis roseipennis
5 = Callieda decora
6 = Miaumenops celar
7 = Hentzia palmerum
8 = Chiracanthium inclusum
9 = Oxyopes salticus
10 = small VBC

[c]Maximum number of predators found in any one sample.

[d]Small VBC with Nomurea rileyi infection.

.00	.00	70 (-82)	30 (-48)	16.30 (7.56)	3	0
00	.00	73 (-80)	.33 (-49)	20 13 (8.38)	-	23
.00	.70 (-95)	20 (.42)	.20 (.42)	11.90 (8.21)	4	7
.00	40 (-70)	30 (-68)	.10 (.32)	10.60 (3.63)	5	25
00	.20 (-42)	-60 (-70)	.30 (-48)	7.20 (2.32)	7	23

Table A.2 Beat cloth sampling data for 1982.

Julian date	Average number				
	1	2	3	4	5
184	.27 (.70)	.07 (.26)	00	.00	.00
188	.13 (.35)	00	.00	.00	.00
191	.33 (.62)	00	00	.00	.00
195	.47 (.64)	.13 (.35)	.00	.00	.00
198	.27 (.46)	.13 (.52)	.00	00	.00
203	.27 (.46)	.00	.07 (.26)	.00	.00
210	.53 (.74)	.13 (.35)	.27 (.46)	.07 (.26)	.07 (.26)
212	.47 (.83)	.20 (.41)	.33 (.62)	.07 (.26)	.07 (.26)
216	.20 (.41)	00	.20 (.56)	.07 (.26)	.07 (.26)
219	.27 (.46)	.00	.13 (.35)	.13 (.35)	.20 (.41)
223	.73 (.59)	.00	.47 (.64)	.07 (.26)	.20 (.41)
226	1.13 (1.60)	.00	.47 (.92)	.07 (.26)	.27 (.59)
231	1.60 (1.35)	.00	.87 (1.06)	.13 (.35)	.20 (.56)
237	.80 (1.01)	.00	.20 (.41)	.40 (.63)	.07 (.26)
240	1.07 (.96)	.00	.07 (.26)	.20 (.56)	.00

Table A.2--extended.

(SD)[a] of species[b]					Maximum number predators[c]	Number diseased small VSC[d]
6	7	8	9	10		
.07 (.26)	.00	.00	.00	.00	3	0
.00	.00	.00	.00	.00	1	0
.00	.00	.00	.00	00	2	0
00	00	.00	.00	00	2	0
.07 (.26)	.00	.00	.07 (.26)	.13 (.35)	3	0
00	.07 (.26)	.07 (.26)	.00	.47 (.64)	2	0
.07 (.26)	.00	.07 (.26)	.07 (.26)	.27 (.59)	3	0
.00	.00	.00	.07 (.26)	.93 (1.22)	4	0
.00	.07 (.26)	.40 (.63)	.00	1.60 (1.24)	4	0
.13 (.35)	.13 (.35)	.40 (.63)	.07 (.26)	4.13 (2.42)	5	0
.00	.07 (.26)	.20 (.41)	.07 (.26)	8.80 (4.62)	4	0
07 (.26)	07 (.26)	.07 (.26)	.07 (.26)	10.60 (5.48)	9	0
07 (.26)	.07 (.26)	40 (.63)	.20 (.56)	8.67 (3.72)	8	1
00	.07 (.26)	.13 (.35)	.00	11.13 (7.03)	5	3
.13 (.35)	20 (.56)	.27 (.59)	.13 (.35)	13.07 (6.86)	7	8

Table A 2

244	.80 (1.01)		.33 (.49)	.20 (.41)	.13 (.35)
247	1.13 (1.30)	.00	.33 (.49)	.13 (.35)	.27 (.59)
251	1.60 (1.55)	.00	.47 (.64)	.27 (.46)	.07 (.26)
254	.87 (.83)	.00	.20 (.56)	.07 (.26)	.33 (.82)
258	1.13 (1.13)	.00	.13 (.35)	.20 (.41)	.27 (.59)
261	.53 (.64)	.00	.00	.27 (.46)	.07 (.26)
265	1.00 (1.51)	.00	.00	.13 (.35)	.20 (.56)
268	1.67 (1.45)	.00	.13 (.50)	.13 (.35)	.27 (.46)
272	.87 (.92)	.00	.00	.33 (.62)	.13 (.50)
277	.60 (.74)	.00	.27 (.46)	.07 (.26)	.07 (.26)

[a] Standard deviation (n = 15).

[b] Species:
1 = Gaocoris punctipes
2 = Geocoris uliginosus
3 = Trobiconabis capaiformis
4 = Nabis roaispennis
5 = Callisda decora
6 = Misumenops celer
7 = Mentzia palmerum
8 = Chiracanthium inclusum
9 = Oxyopes salticus
10 = small VSC

[c] Maximum number of predators found in any one sample.

[d] Small VSC with Nomurea rileyi infection.

.00	.13 (.35)	.13 (.35)	.07 (.26)	13.87 (9.31)	5	41
.00	.13 (.35)	.53 (1.06)	.07 (.26)	17.53 (9.83)	7	66
.00	.27 (.59)	.40 (.51)	.07 (.26)	8.00 (4.11)	9	9
.13 (.35)	.13 (.35)	.40 (.63)	.07 (.26)	2.40 (1.96)	5	34
.07 (.26)	.20 (.56)	.20 (.41)	.07 (.26)	2.87 (2.70)	6	11
.00	.20 (.41)	.20 (.41)	.13 (.35)	8.53 (5.26)	4	10
.00	.13 (.35)	.13 (.35)	.13 (.50)	4.27 (2.63)	6	7
.07 (.26)	.13 (.35)	.27 (.46)	.00	2.73 (2.02)	8	15
.07 (.26)	.07 (.26)	.07 (.26)	.13 (.35)	3.60 (2.59)	4	6
.00	.00	.20 (.56)	.00	4.47 (2.75)	6	7

APPENDIX B
LEAF AREA ESTIMATION FOR 1981

Leaf area was not directly measured via field samples in 1981. Instead, the Soybean Integrated Crop Management (SICM) model (Wilkerson et al. 1983) was used to estimate the leaf area in 1981. The SICM model is a computer simulation model of soybean production including a mechanistic soybean plant sub-model (Wilkerson et al. 1983). Driven by biotic and abiotic components, the soybean plant sub-model describes the changes in leaf area through time. The rate of growth of the leaf area is site specific--dependent on the conditions of particular soybean fields. By incorporating the relevant weather, agronomic, and VRC variables specific to Green Acres Agronomy Farm in 1981 into the SICM model, an accurate estimate of the leaf area in 1981 can be obtained.

The variables that govern plant growth in the SICM model are:

(1) minimum and maximum daily temperature (°C)
(2) day length (hours)
(3) solar radiation (langleys)
(4) photosynthetically active radiation (PAR) einstiens/m^2)
(5) pan evaporation

(6) rainfall (cm)

(7) number of small, medium, and large VBC per 91 cm of soybean row

(8) planting date

(9) row spacing (cm)

(10) planting density (number plants per m^2)

Rainfall, VBC densities, and the agronomic data (8-10 above) were measured directly at Green Acres (see Chapter V). Temperature, solar radiation, PAR, and pan evaporation were measured by the National Weather Service at a site located approximately 17 km southeast of Green Acres on the campus of the University of Florida, Gainesville, Florida.

As described in Chapter II, the SICM model couples VBC dynamics and soybean growth to estimate the impact of VBC populations on soybean ontogeny and yield. Since VBC larvae consume leaf area, the number of VBC (especially the medium and large VBC: see Luna 1979) present will effect the total leaf area present. To estimate the leaf area in 1981, the description of the number of VBC (all larval stages) through time in the SICM model was set equal to the measured (see Table A.1) densities of VBC in the field. Linear interpolation was used to estimate VBC densities between sampling dates. To judge how well the SICM model predicts the leaf area using this technique, the relevant variable estimates for Green Acres 1982 were input into the SICM model, and the predicted leaf area was compared to the leaf area measured in 1982. As seen from Figure 5.4, the SICM

model can be used to accurately estimate the leaf area for a given site. Additional validation of the model is given in Wilkerson et al. (1983).

After confirming the utility of the SICM model in predicting leaf area, the variable estimates for Green Acres 1981 were input into the SICM model and the leaf area for 1981 estimated. Figure 5.5 shows the estimated leaf area per 91 cm of soybean row for 1981.

APPENDIX C
DATA FROM EXPERIMENTS

Table C.1. Data from each replicate in 1981

Julian date	Treatment[a]	Number plants[b] Replicate Number 1	2	3	-- Number per species[c] -- 1	2	3	4	5	6	7	8	9	Predation rate[d] Replicate number 1	2	3
232[e]	NL	24	24	24	1	1	1		1	1	1		2	2.75	2.75	0.00
	A1	24	24	24	1	2	1		1	1	2		1	2.75	0.00	0.00
	A2													0.00	0.00	0.00
	MX	24	24	24	1	1	1		1	1	1		1	3.75	4.75	4.75
	MN															
246[f]	NL	22	19	24	2		1	1				1	1	0.00	0.00	0.00
	A1	24	24	24	2		2	1				1	1	3.33	0.00	0.00
	A2	24	24	24	3		3	2				1	1	1.33	1.33	0.00
	MX	25	24	24	1		1	1				1	1	1.33	0.00	0.00
	MN															
253	NL	24	24	24	5		1	2	1				2	5.00	4.00	3.00
	A1	24	24	24	3		2	1	1				1	7.00	4.00	0.00
	A2	24	25	24	2		1	1	1				1	4.00	3.00	8.00
	MX	24	24	24	1		1	1	1				1	2.00	4.00	0.00
	MN	24	24	24	12									1.00	5.00	3.00
260	NL	22	24	24	6		1		1		1		2	5.00	2.00	6.00
	A1	28	24	24	2		2		1		1		1	2.00	4.00	3.00
	A2	27	24	24	3		3		1		1		3	6.00	7.00	8.00
	MX	24	24	24	1		1		1		1		1	3.00	4.00	0.00
	MN	24	24	24	13									5.00	6.00	7.00

267	NL	24	24	24	2	2	1	1	1	2	2	2.67	6.67	1.67
	A1	24	24	24	3	3	1	1	1	1	2	1.67	2.67	0.00
	A2	24	24	24	4	1	1	2	1	1	1	2.67	2.67	1.67
	MX	24	24	24	1	1	1	1	1	1	1	2.67	0.00	0.00
	MN	30	24	24	9							1.67	0.00	0.00

[a]Treatment abbreviations: NL = normal, A1 = Alternative 1, A2 = alternative I1. MX = maximum, MN = minimum.

[b]Number plants per cage = 24 unless otherwise noted.

[c]Species

1 = Geocoris punctipes
2 = Geocoris uliginosus
3 = Trobiconabis capsiformis
4 = Nabis roseipennis
5 = Callieda decora
6 = Misumenops celer
7 = Oxyopes salticus
8 = Hentzia palmarum
9 = Chiracanthium inclusum

[d]Predation rates less than 1.00 are set to 0.00.

[e]Fourth NL and MX replicate = 0.00 attacks with 24 plants. No A2 or MN treatment this week.

[f]No MN treatment this week.

Table C.2. Data from each replicate in 1982.

Julian Date	Treatment[a]	Number plants[b]			-- Number per species[c] --									Predation rate[d]		
		Replicate number			1	2	3	4	5	6	7	8	9	Replicate number		
		1	2	3										1	2	3
196	NL	11	16	25	5									1.33	0.00	0.00
	T1	14	15	13	4						1			1.33	2.33	0.00
	T2	15	16	10	3			1			1			3.33	0.00	0.00
	T3	14	17	12	2		1	1			1			1.33	4.33	0.00
	T4	12	24	22	1	1	1	1			1			1.33	3.33	1.33
204	NL	15	13	15	5						2			1.00	3.00	0.00
	T1	13	12	17	4		1				2			2.00	0.00	0.00
	T2	18	14	19	5		1				1			4.00	0.00	0.00
	T3	13	16	13	3	1	1	1	1					0.00	0.00	0.00
	T4	16	15	12	1	1	1	1	1	1	1			1.00	1.00	0.00
210	NL	16	14	19	4	1	1				2			0.00	0.00	0.00
	T1	14	18	16	4	1	2				1			4.33	1.33	0.00
	T2	23	12	15	5	1	1				1			2.33	0.00	0.00
	T3	16	19	14	2	1	1	1	2	1				0.00	0.00	0.00
	T4	15	10	15	2	1	1		1	1	1		1	2.33	0.00	0.00
217	NL	14	10	19	1		2	1	1			1	2	2.67	0.00	0.00
	T1	18	19	12	2	1	2		2		1			2.67	3.67	0.00
	T2	11	15	12	2	2	1		1		2			1.67	1.67	0.00
	T3	12	17	19	3	1	2		1		1			1.67	0.00	0.00
	T4	7	16	15	2	2	1		1	1	1			1.67	0.00	0.00

Table C 2--continued

224	NL	16	13	13	2		2	1	1		1	1	1	5.00	1.00	0.00
	T1	16	12	12	3		2	2	1	1				2.00	3.00	0.00
	T2	15	13	12	4		2	1	1	1				3.00	6.00	0.00
	T3	12	18	14	6			1	1	1				4.00	1.00	1.00
	T4	13	14	22	4		2		1		1		1	3.00	3.00	0.00
231	NL	14	20	16	2	1	1		1	1	1	1		3.00	0.00	0.00
	T1	10	15	14	2		2		2	1			1	1.00	0.00	0.00
	T2	17	17	14	3		3		1				1	4.00	1.00	2.00
	T3	18	16	14	3		2		2				1	3.00	1.00	6.00
	T4	15	19	13	3		2	1	2					2.00	6.00	1.00
238	NL	10	13	12	3		1	2	1			1	1	7.67	4.67	0.00
	T1	13	14	18	3	1	2		2			1		2.67	0.00	0.00
	T2	13	13	9	3	1	2		1	1	1			3.67	0.00	0.00
	T3	12	22	12	3		3		2	1				2.67	0.00	0.00
	T4	13	13	14	3		3		1	1			1	0.00	0.00	0.00
245	NL	17	14	12	3		1	1	1		1	1	1	4.67	1.67	5.67
	T1	10	25	20	2		2	1	2	1		1		2.67	5.67	1.67
	T2	14	9	14	1	1	3	1	2		1			8.67	2.67	9.67
	T3	17	17	13	2	1	2	1	1	1			1	3.67	7.67	1.67
	T4	13	16	14	2		2		2		1	1	1	2.67	5.67	5.67
259	NL	13	13	9	2		1	1	2	1	1	2	1	3.00	5.00	0.00
	T1	17	16	9	4		2		1	1		2	1	3.00	1.00	0.00
	T2	15	12	15	5	2		1	1	1	1			0.00	0.00	0.00
	T3	9	19	13	4		2	1	2			1	1	4.00	6.00	4.00
	T4	16	9	12	5		1	1	1			1	2	3.00	3.00	0.00

Table C 2--continued

266	NL	17	12	14	3	1	1	2		1	1	2	1.67	2.67	0.00
	T1	10	21	13	3	1	1	3	1		2		4.67	2.67	4.67
	T2	14	18	16	5		1	2	1		1	1	1.67	1.67	0.00
	T3	17	12	13	4	1	1	3			1	1	3.67	4.67	4.67
	T4	15	14	13	3	1		3	2		1	1	1.67	2.67	3.67
273	NL	17	18	15	1	1		1	1	1			2.67	0.00	0.00
	T1	14	12	12			1	2			1	1	1.67	3.67	0.00
	T2	10	15	10	2			1			1	1	1.67	0.00	0.00
	T3	14	10	23			1	3				1	1.67	0.00	0.00
	T4	23	14	18	2		1	1				1	1.67	1.67	4.67

[a]Treatment abbreviations: NL = normal, T1-T4 = alternative treatments.

[b]Number plants per cage

[c]Species:
1 = Geocoris punctipes
2 = Geocoris uliginosus
3 = Trobiconabia capsiformis
4 = Nabis roseipennis
5 = Callieda decora
6 = Miaumenops celer
7 = Oxyopes salticus
8 = Hentzia palmerum
9 = Chiracanthium inclusum

[d]Predation rates less than 1.00 are set to 0.00

APPENDIX D
FORTRAN CODE FOR DYNAMICS MODEL

```
C INITIAL CONDITIONS

      XLEAF=7700
      BCK=.15
      XJP=.08
      VBC=0.
      GROLF=1408.
      GROVBC= 175
      GROPRD=0.05
      PRED= 40
      XNR=0.0
      XJH=0
      DT=1
      T=180

C LEAF AREA DESCRIPTION

   10 T=DT+T
      IF(T.LE.222.)XLEAF=XLEAF+GROLF
      IF(T.GE.223. .AND. T.LE.236.) XLEAF=XLEAF
      IF(T.GT.236. .AND. T.LT.294.)XLEAF=XLEAF-439.
      IF(T.EQ.294.)XMAXLF=XLEAF
      IF(T.GE.294.)XLEAF=XMAXLF*EXP(-(T-294.)/2.0)
      IF(XLEAF.LE. 0.0)XLEAF=1.0

C VBC DESCRIPTION

      XKP=.4515*EXP(-5045./VBC/XLEAF)+400.
      IF (T.GE. 215.)XJH=1.00
      IF(VBC/XLEAF .GE. .000275 .AND. T .GE.244) XNR=.15
      VBC=VBC +XJH +GROVBC*VBC
     %-VBC*XKP*PRED/XLEAF-XNR*VBC-BCK*VBC
      IF(VBC LE.0.)VBC=0.

C PREDATOR DESCRIPTION

      PRED=PRED+XJP +GROPRD*VBC*XKP*PRED/XLEAF
     %    -.05*PRED
      IF(PRED.LE. 0.0)PRED=0.0
```

```
C DEFINITIONS

C XLEAF:  leaf area in cm^2 both leaf sides
C BCK:  daily proportional background mortality rate of
        small VBC.
C XJP:  predators daily net migration rate, number/day/91
        cm of soybean row.
C VBC:  number of small VBC per 91 cm of soybean row.
C GROLF:  daily increase in leaf area in cm^2
C GROVBC:  daily proportional small VBC population growth
           rate;
C GROPRD:  conversion rate of ingested small VBC to predator
           offspring.
C PRED:  number of small VBC predators per 91 cm of soybean
         row;
C XNT:  daily proportional disease mortality rate of small
        VBC.
C XJH:  small VBC daily net migration rate, number/day/91
        cm of soybean row.
C DT:  change in time; temporal resolution of model (one
       day)
C T:  time in days (Julian)
C XMALF:  maximum leaf area.
C EXP:  base of the natural logarithm.
C XKP:  amount of leaf area searched per predator in cm^2.
```

BIOGRAPHICAL SKETCH

Robert James O'Neil was born July 14, 1955, in Boston, Massachusetts. Robert attended and graduated from Belmont High School in 1973. He enrolled at The University of Massachusetts, Amherst, and received his Bachelor of Science degree in entomology in 1977. Robert continued his education at Texas A&M University, College Station, and received his Master of Science degree in entomology in 1980. He enrolled at The University of Florida, Gainesville, in August 1980. Robert is married to Elizabeth McDonough, and they have one child, Jennifer Anne.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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